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P.A. GAYDECKI

A Quantification of the Behavioural Dynamics of Certain Lepidoptera in Response to Light

Supervisor: Professor G.W. Schaefer

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ABSTRACT

Many types of insect, in particular the nocturnal Lepidoptera, will fly towards artificial sources of illumination. Such animals are often described as being positively phototactic, but although little progress has been made towards a fundamental understanding of this phenomenon, its existence continues to be exploited with the use of light-traps. This thesis attempts to explain, in part, why certain British night-flying Lepidoptera are caught, or fly close to, light-traps. The experimentation and analysis has been structured into three separate but inter-related studies. The first is an investigation into the effects that weather factors exert on light-trap catch. Standard analytical procedures were extended to reveal that sensitivity to these factors is related to insect size and gross morphology. The second of these studies is an analysis of the types of moth flight pattern produced when these insects are exposed to various forms of illumination under field conditions. Moth tracks were recorded on video with the help of image intensification, and the frame-by-frame co-ordinates transferred to, and processed by, a microcomputer, which produced matrix maps of speeds, accelerations and time-surface densities around a light-trap. Instantaneous windspeeds were recorded. The dynamical analysis suggests that moth flight towards light arises primarily from a misinterpretation of the stimulus, competing at short distances with a strong escape response, thus evoking a profound state of disorientation. Furthermore, the data indicated that the types of pattern found were species linked. In the third study, a remote-sensing technique was used to quantify moth aerial density, which was compared with simultaneous light-trap catches nearby, giving an estimate of absolute trap catching efficiency under various meteorological conditions. Because of their mode of operation, and their increasing loss of effectiveness in higher windspeeds, light-traps have only a limited capacity to reflect aerial density.

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GENERAL INTRODUCTION

Behavioural biology is an extraordinarily complex science. In certain branches of physics, for example, the outcome of an experiment may be estimated with such accuracy that statistical examination is an irrelevancy. Animal behaviour is not controlled by readily understandable forces, but at one level by neuro-physiological processes about which we know only vague generalities. Because of the daunting nature of this problem, many behavioural hypotheses are tentative and applicable only in specific cases. The root cause of this dilemma is lack of communication - we cannot ask an organism why it performed a particular action, and so we reply on inference and our powers of deduction. Realising the limitations of these tools, we necessarily attach probabilities to our predictions concerning what an animal may or may not do under certain conditions.

The study of insect behaviour is less hampered by this problem than is the study of the behaviour of higher organisms, as many forms of insect behaviour are instinctive and only slightly modified by learning. Nevertheless, control or monitoring of insect populations is often accomplished by the application of a set of observed regularities about a species' behaviour without understanding the reasons behind them. Light-trapping of insects is a case in point. Light-traps are used in many countries to measure the level of infestation of a species or to record the numbers and types of insects in a given area, and much work has been published on this basis. The reasons why insects, and in particular moths, are affected by light are often ignored or are briefly mentioned as being attributable to a phototactic reaction.

The primary aim of this study, which was conducted from the years 1981-1983 inclusive, was to examine in detail the dynamic changes which took place in the flight tracks of moths when close to a light source. This aim was a major component of a study comprising three interlinked categories:

1. the influence of weather factors upon light-trap catch and their effects upon moth behaviour;

2. the monitoring of moth flight behaviour in response to light, using suitable video imaging and processing apparatus;

3. the calibration of light-trap catches and the estimation of moth aerial density using the monitoring techniques mentioned above.

The real-time monitoring of insects in flight is not a new biological method; photographic, cinematographic and video techniques have all been employed at various times in the past. The originality of this work did not depend upon the kind of monitoring equipment used, but upon the subject matter and the subsequent processing of the video-recorded images. This was made possible by the use of infra-red imaging devices available in the Group, and by the advances made in recent years in the field of microelectronics. Biological research is often dependent upon rather limited funding, and much can be achieved by the judicious use of low-cost microcomputers.

The use of a microcomputer forming the core of an inexpensive entomological tracking system is not without precedent. Bent (1982) describes the construction and application of a video imaging system using an Apple IIe, which could extract the x and y co-ordinates of insects flying against a mid-day sky, in real time. A total of eight independent flight trajectories could be tracked at any instant, with a digitizing rate of 50Hz. In the present work a different method of digitizing was employed (since it was performed on video-recorded tracks), although the effective conversion rate was the same. In the year that the monitoring of moth flight behaviour took place - 1982 - Hoy et al. developed a video digitizing system interfacing to an Apple IIe, specifically to aid behavioural observations.

This system could only process an organism's x and y co-ordinates six times per second (as compared to fifty in this case), and was only useful for recording the behaviour of animals with a maximum speed of three body lengths per second. It was therefore a laboratory rather than a fieldwork aid. Nocturnal Lepidoptera, whose body length for the larger noctuids may be typically 3cm, and whose flight speed is roughly 2m/s, move at a rate of about 67 body lengths per second.

Although considerable effort has been made to integrate the three years' work under the general heading of "behaviour", each category listed above is usually treated quite separately in the literature which has been published on these topics. In order to facilitate the flow of ideas, no formal literature survey is contained in this Introduction but appears in the relevant discussions for each year.

A Brief Description of the Lepidopteran Visual System

With regard to light, a moth may only modify its behaviour by acting upon information received through its visual system. A basic understanding of this system is therefore an important part of any discussion concerned with these behavioural modifications, since, as will be seen later, certain types of actions are directly attributable to physiological changes which occur under different levels of illumination. Lepidoptera possess highly developed visual systems, and like other insects, this vision is mediated primarily by the single pair of compound eyes and to a lesser extent by the dorsal ocelli (Figure 1a). The function of the dorsal ocelli is not entirely clear, since they may in certain species be concealed by scales, or be absent from the surface as they are located within the head (Eaton, 1971). It is known that they act as both synergists and antagonists with regard to phototaxis, but this again is species related.

Not only is their visual field overlapped by that of the compound eyes, but the principle focal plane of the lens falls below the level of the retinal layer. Furthermore, many retinal cells converge onto a much smaller number of ocellar nerve fibres, so making it extremely unlikely that the dorsal ocelli can mediate the perception of form. Electrophysilogical evidence strongly supports the theory that they are sensitive to the changing intensity of light, and it is generally accepted that they are stimulatory organs, functioning to raise the excitory level of the insect in conjunction with the images received by the compound eyes (Ruck, 1961).

Unlike the dorsal ocelli, the exterior of the compound eye is divided into numerous facets, each facet being assigned to a single ocellus. These separate visual elements are known as ommatidia, and the numbers present vary greatly in different orders. Only Odonata (dragonflies and damselflies) possess more ommatidia per compound eye than the Lepidoptera - from 10,000 to 28,000, as compared with 12,000 to 17,000. These facets are not always of equal dimension over the surface of the eye, and so the angle of perception varies. Because of the overlap of the visual field for each ommatidia, insects do not perceive form in the same manner as mammals, although the precise nature of its representation is the subject of considerable debate.

The outermost layer of the ommatidium, the cornea (see Figures 1b and 1c) is formed of a transparent cuticle acting as a lens. It is bi-convex in cross-section and the refractive index decreases from the centre outwards to correct for chromatic aberration. Although many orders of insects possess a smooth corneal surface, the Lepidopteran eye is covered with numerous cone-like hairs projecting from between the ommatidia - the corneal nipple array - which serves the same purpose as the coating on a lens; it reduces reflection at the surface and increases the transmission of light through the cornea. The cornea may develop as a secretion from the cornegean layer, which is that part of the epidermis extending below the cornea. This is not always

present, in which case the cornea is secreted directly by the crystalline cone cells. These four crystalline cone cells which enable the transport of metabolites to the ommatidia (Horridge and Giddings, 1971), are surrounded by the primary pigment cells, sometimes known as the primary iris cells. The bases of these elongate to form the crystalline tract (which varies in length according to whether the eye is light or dark-adapted), transmitting light to the distal retinula cells and thence to the eight proximal retinula cells. The rhabdom is formed from eight rhabdomeres, which consist of numerous microvilli, projecting from the surface of the retinula cells. These rhabdomeres fuse to form as single pigmented (rhodopsin) rhabdom which is attached by nerve fibres to the central nervous system.

The whole system operates by the triggering of nerve impulses by the rhabdom as the rhodopsin undergoes photochemical breakdown upon exposure to light. The simple mosaic theory of visual perception, first proposed by Johhanes Muller in 1829, states that each ommatidium responds to a fraction of the image, and the combination of these fractions results in the formation of a complete image similar to a low resolution photograph. Because each ommatidium commonly receives light from a wider angle than it subtends geometrically, it is unlikely that the final image will be a sum of the individual components. Moreover, like the mammalian eye, numerous retinular nerve fibres interlink or divide into several branches, which suggests that the central nervous system possesses a very elaborate image processing system (from Richards and Davies, 1977).

As Figures 1b and 1c show, the primary pigmental cells vary in length according to the intensity of light, and they therefore control how much light the adjacent ommatidia will receive from a corneal facet. In situations of low light intensity, the pigmental cells are withdrawn and more ommatidia will be stimulated than just the one whose axis is parallel to that of the incident light. This process may typically take between ten and fifteen minutes (Walcott, 1975). Thus nocturnally active insects

sacrifice acuity for sensitivity of vision, a phenomenon which is also common to the mammalian eye.

The Mediation of Vision and Communication by Other Structures

Although the work which is described in this thesis was not involved directly with the Lepidopteran response to infra-red emissions, near infra-red beams (780nm and above) were used as a field calibration tool to enable the estimation of moth aerial density in the final year. In order for this method to be reliable, it was necessary that the frequencies used interfered as little as possible with the normal activity of the moths. In the past moths were considered to be insensitive to such frequencies, but in 1965 Callahan proposed that the antennal pectinations of certain moths may act as dielectric rod antennae which are of the length to be sensitive to thermal infra-red frequencies. These frequencies are emitted as black-body radiations from individual moths, possibly modulated by wing-beating or, in the case of females, by the posterior segments of the abdomen. They are also produced as specific emissions of pheromone molecules. As this signal passes through the atmosphere its intensity would be attenuated and its spectrum filtered by selective atmospheric absorption. Thus a male from a particular species might recognise a certain bandwidth and respond accordingly. This theory has been tested in two ways. Firstly, moths were tethered within a wind tunnel and their reactions noted to the pheromones of the female and to the infra-red emissions of the correct bandwidth and intensity. Hsiao (1972) performed the experiment with meticulous care, generating infra-red radiation modulated according to the wing-beat rate of the moth (Trichoplusia ni), and filtering it to correspond as nearly as possible to the emission signature of the pheromone (from 1 to 15μm, with troughs at 3.3, 5.6, 7.3, 8 and 9.6μm). The response to the pheromone was unquestionable, eliciting a sharp rise in the wing-beat rate and in the forward force exerted. When the infra-red signal was substituted, there

was no hint of a reaction, even after increasing the intensity of emission.

The second set of experiments (Hsiao and Hackwell, 1970), was designed to test the ability of the antennae to detect artificial sources of light, perhaps by responding to their infra-red component. Blinding the moths (Heliothis zea) produced a complete inhibition of the phototactic resonse towards a tungsten source, but removal of the antennae made no difference. Hsiao does not state categorically that the infra-red detection ability of Lepidoptera is non-existent, only that it has yet to be demonstrated in the laboratory. He also states that although there is sufficient thermal energy emitted by pheromone molecules released from a female to be detected, the interference from water molecules in the atmosphere exceeds this by 170dB (a factor of 10^{17}).

This issue is certainly not a closed subject, but it is probable that for many species of moth, the sensitivity in this region is low. The subject of Lepidopteran vision is vast, both at a physiological and behavioural level however, and research continues not only with respect to infra-red sensitivity, but over many aspects of the Lepidopteran response to visual stimuli.

CHAPTER ONE

THE INFLUENCE OF METEOROLOGY UPON LIGHT-TRAP CATCHES OF MOTHS, AND ITS RELATIONSHIP TO INSECT SIZE (1981 Analysis)

1.1. Introduction

Between the years of 1936 and 1940, C.B. Williams (1939, 1940) conducted what is generally considered to have been the first major analysis of the way in which light-trap catches of insects are influenced by weather conditions. Since that time innumerable studies have investigated the performance of these devices against a host of meteorological, environmental and biological factors.

The purpose of the 1981 fieldwork - the quantification of trapping variability for different Lepidopterous species under changing meteorological conditions - may at first sight appear repetitious or even redundant, until some of the rationale behind the experimentation is explained. Most work previously concerned with this topic has concentrated on the total nightly catch of a single species, or, as in the case of Williams in 1940, total nightly catch of all insects regardless of species. In this study, not only was total nightly catch of certain species correlated with such factors as temperature, windspeed and humidity, but an attempt was made to view these relationships in context with the nightly activity of those species. This was possible since, during its time of operation, the trap was emptied every half hour for a total of nineteen nights. Furthermore, instead of merely describing the associations between weather and nocturnally active Lepidoptera - albeit statistically - a range of species which had similar annual flight periods but different bodily dimensions were chosen in order to investigate how these associations would alter in relation

to the physiology of the insect. It was hoped that underlying principles would be uncovered rather than just a set of population coefficients relevant only to the year in which the fieldwork was undertaken. Such coefficients would clearly be inapplicable for a year when the population of a given species was appreciably different from that in which the work was performed.

In order to maximise the effect of the weather variables, trapping was carried out in an exposed location rather than in a wood or garden. Although it is usual - when a range of species are of interest - to operate a light-trap in an area where cover is provided by the surround vegetation, this was deliberately avoided for that reason. Sheltered areas not only reduce the impact of wind, but under certain conditions give rise to turbulence which is difficult to examine on a statistical basis when analysing trap catch. Moreover, because nocturnal Lepidoptera seek protection during the day under tree bark or unobtrusive locations in the undergrowth, light-traps placed in wooded areas tend to catch a highly local population which might be completely unrepresentative of the species and numbers of moths on the wing over large tracts of crop or grassland.

1.2. Choice of trapping times and location

In 1981 a Robinson pattern trap (Robinson and Robinson, 1950) using a 125W MV lamp and placed at 1.4m above ground level (as measured from the mid-point of the lamp), was operating almost on a daily basis at Cranfield from the 15th March to the 30th July. The positioning of the trap is shown by the map of Figure 2. No statistical analysis was performed on the accumulated data, but rather the purpose of this trapping was to acquaint the experimenter with the species indigenous to this area.

On the 10th August this light-trap was moved to a second location (again shown on the map) which was considerably more exposed, since it was positioned on an uncut grass strip extending over 100m into a field of wheat; the nearest buildings of a size likely to be of significance regarding competitive illumination and wind influence were situated on a housing estate lying to the south-east of the trap at a distance of approximately 150m. The trap was operated on a nightly basis from the 10th to the 30th August, with the exception of the 15th and 16th, i.e., for a total of 19 nights. Sampling would commence at 20.30 BST and finish at 03.30 BST, during which the trap was emptied and the catch sorted every half hour, thus providing fourteen catch periods per night.

1.3. Data recording

a) Biological data

Identification was carried out for all of the Lepidopterous species which entered the trap, but four species of Noctuidae and certain other species of Pyralidae were of most interest. The former included Noctua pronuba, Noctua comes, Noctua janthina and Mesapamea secalis. Of the Pyralidae, all were of the kind loosely described as microlepidoptera, and the vast majority of these (90%) were Agriphilia tristella.

b) Meteorological data

The Ecological Physics Research Group at Cranfield operates its own weather station (to Meteorological Office standard) from the beginning of spring until the end of autumn, and a record was kept of the following:

i) temperature - a Casella thermohygrograph recorded temperature (Celsius) to an accuracy of 0.5 degrees on a paper chart changed daily. This was checked at regular intervals by a standard dry bulb thermometer as well as maximum and minimum thermometers;

ii) humidity - the same instrument also recorded relative humidity to a resolution of 5%, checked against wet and dry thermometers;

iii) air movement - this was measured at a height of 10m using a Munro cup-and-vane anemometer, recorded on a continuous feed strip chart;

iv) rainfall - both a Casella chart recorder and a funnel check gauge were used for this purpose. The check gauge had a minimum resolution of 0.1mm;

v) barometric pressure - this was monitored on a Casella barograph chart recorder and checked against a standard mercury barometer with a resolution of 0.1 millibars;

vi) ambient light levels - during the period of sampling, light intensity in Lux was measured at half hourly intervals using a Minilux 100 linear meter, which had a detection threshold of 0.01 Lux. The sensor for this device is a sub-divided selenium cell, which is both colour and cosine corrected; it therefore has a similar spectral sensitivity to that of the human eye.

1.4. Transfer of data to computer files (floppy disc)

Tables 1a and 1b provide details of the way in which the biological and meteorological data was compiled and subsequently entered into computer memory to be stored on floppy disc. These files comprise two categories; the first contains totals of a particular species for each night, or averages of a measured parameter over a twelve hour period, for both day and night. The second category for both biological and meteorological data all contains fourteen values, corresponding to the fourteen half hourly sample periods of each night. For each species therefore, any value (e.g. numbers of N. pronuba captured between 22.30 and 23.00 hours) will be a mean of the numbers caught at that time period for the nineteen nights, normalised to a percentage of the total catch for that species. For the meteorological data in this category, the files contain information relating to the way in which conditions changed over a single typical night, again produced by averaging the half hourly readings for the nineteen nights.

During the early stages of analysis involving wind data, calculations were based upon the original values obtained from the air movement at 10m. These calculations were lated repeated with the wind data files corrected for equivalent speeds at a height of 2m above a fully grown wheat crop (Pinnock, 1983), since the work was performed just prior to the harvest. This was done in order to standardise comparisons withthe calibration work of 1983, when all windspeeds were measured at 2m. These revised calculations (for the 1981 data) actually produced better correlations than those performed with the unmodified readings.

TABLE 1a

Diurnal Meteorological and Biological Data

Variable	Units	Time period (BST)	Time between measurements	No. measurements per average
Mean daily temp.	^{o}C	08.00-20.00	30 mins.	24
" " windspeed	m/s	"	"	"
" " humidity	R.H.	"	"	"
" " pressure	$mb-10^{3}$	"	1 hr.	12
" nightly temp.	^{o}C	20.00-08.00	30 mins.	24
" " windspeed	m/s	"	"	"
" " humidity	R.H.	"	"	"
" " pressure	$mb-10^{3}$	"	1 hr.	12
Daily rainfall	mm	08.00-20.00	12 hr.	-
Nightly rainfall	mm	20.00-08.00	"	-
" illuminance	Lux	21.00-03.00	30 mins.	-
Total nightly catch (individual species)	Nos.	20.30-03.30	30 mins.	-

Note: Maximum and minimum temperatures (both daily and nightly) were recorded and stored separately.

TABLE 1b

Half-hourly Meteorological and Biological Data

Sample period: 20.30-03.30 BST
No. of Readings: 14

Variable	Units
Temperature	^{o}C
Windspeed	m/s
Humidity	R.H.
Pressure	$mb-10^{3}$
Illuminance	Lux
Trap catch (individual species)	Numbers

1.5. Forms of Analysis

In most cases when it is necessary to quantify the degree of association between two variables, such as numbers of an insect species caught in a light-trap against temperature during the time of operation, regression analysis is the most commonly used test. Regression analysis can take a number of forms - it may be a simple linear fit involving one dependent and one independent variable, or it may include a number of non-linear independent variables (multivariate curvilinear regression). For any of these methods to be valid as a statistical tool, two preconditions must be satisfied with respect to the dependent variable before analysis can proceed:

1) for any fixed value of the independent variable, the corresponding values of the dependent variable that would arise from repeated samples should follow a normal distribution;

ii) the variance, or spread of these distributions, should not alter significantly with changing values of the independent variable.

The second of these conditions is not usually a problem when dealing with large biological samples, but the first condition may very well necessitate the data to be normalised in some fashion. This is because insect populations, especially those of Lepidopterious species, are subject to extreme density variability over the course of a season or year; thus any apparent association between numbers trapped and a meteorological parameter may in reality be simply due to a change in the local background population which is flight-ready. Although precautions can be taken to ensure that most of the trapping variability is only dependent upon climatic factors, it is never the case that the background population remains perfectly static, and this must be taken into account during the analysis. One method of minimising this source of error is to study only those species which are univoltine, and have a flight period which exceeds the span of the sample period (both before and after) by at least two weeks. In this case, the five species which were most closely studied were not only chosen because of the similarities in their flight periods, but also because they represented a range of sizes which could be related to activity. All of the Noctuids listed below fly in a single generation (Novak, 1980, South, 1961); whilst A. tristella is also univoltine, the individual emergence times of the adults are not closely synchronised and so the number of flight-ready individuals varies during its flight period. (Hollingsworth, pers. comm.). This species lives for not more than two weeks in the adult stage, yet the flight period is over three months in duration. The biological details of these species may be briefly summarised as follows (from Novak, 1980):

1) Agriphila tristella. Wingspan: 23-26mm.
Flight period: June to September. Food Plants: grasses.
Abundant in lowlands.

2) Mesapamea secalis. Wingspan: 27-30mm.
Flight period: July to September. Food Plants: grasses,
corn. Abundant in lowlands.

3) Noctua janthina. Wingspan: 30-40mm.
Flight period: July to September. Food Plants: polyphagous.
Thermophilic species, abundant in lowland regions.

4) Noctua comes. Wingspan: 37-45mm. Flight period: July
to September. Food Plants: polyphagous. Moderately
abundant, favouring agricultural countryside and low
lying submontane meadows.

5) Noctua pronuba. Wingspan: 45-55mm. Flight period: June
to October. Food Plants: polyphagous.

Once the data-base had been compiled, the initial task of analysis was begun, which simply involved graphical inspection of the meteorological and catch trends. Since the graphical process was computerised, the early stages of eliminating potentially unfruitful avenues of investigation were rapidly completed.

The analysis was then given a more quantitative base with the writing of a suite of statistical programmes which performed the following:

1) automatic statistical comparisons (linear regression and probability levels) upon all of the data chosen by the foregoing inspection, with print suppression for any non-significant values. This was a further refinement of the data selection process.

2) Log./linear single variable regressions and associated statistics upon those files selected by Stage (1) above. This determined more precisely the type of relationship which existed in each comparison. Certain biological models make use of the most simple linear regression formula, i.e:

$$n = a + bv \qquad (1)$$

when n represents numbers in a given population,
v is some environmental parameter,
b is the slope coefficient (also called the regression coefficient) and
a is the intercept constant.

Such a model has, however, a very limited usefulness. Firstly, it is invariably the case that more than one factor is involved in controlling the numbers of a population, hence not all of the variance can be accounted for. Secondly, v may not be totally independent but may be influenced by other factors, and so its true effect will be masked. Perhaps most importantly, the value of b is determined by absolute numbers and will therefore change as the population changes. Thus it says nothing about the behavioural associations linking n to v.
As will be seen later in the discussion, the relationships which govern the numbers of Lepidoptera caught in a light-trap are rarely linear with respect to factors such as air temperature and windspeed. In such cases, the form

$$\ln(\text{catch} + 1) = a + bv \qquad (2)$$

may be used. Of particular value in this case is the slope coefficient b, which describes how catch changes with v, independently of absolute numbers (which is determined only by a, the constant). Thus, if b is 0.693 for instance, and v represents temperature, then the catch doubles for every 1^{o} rise; b is therefore a measure of the sensitivity of a population to changes in v.

3) Once the most important factors in controlling the catch had been identified, the final programme in this package combined these factors into a multivariate expression:

$$\ln(\text{catch} + 1) = a + b_1 v_1 \ldots\ldots + b_n v_n.$$

such an equation may be applied for linear interpolation by the following rearrangement:

$$\text{catch} + 1 = e^{a + b_1 v_1 \ldots\ldots + b_n v_n}$$

or

$$\text{catch} + 1 = A.e^{b_1 v_1} \ldots\ldots . e^{b_n v_n}$$

(where $A = e^{a}$).

It may be argued that the writing of such a package was unnecessary since may commercial statistical programmes, such as SPSS, are readily available. However, these programmes were designed for the specific function of processing the 1981 data, and because of compatability between the various routines, the statistical treatment was completed as quickly as possible allowing more time for interpretation of the results.

1.6. Results of the 1981 Analysis

During the three weeks of fieldwork, over thirty different species were identified, but the five species upon which most of the study was concentrated comprised 62.1% of the total numbers caught. The five histograms 3a to 4a show how each species catch changed from night to night, from the 10th to 30th August, with the exceptions of the 15th and 16th. All of these histograms have peaks occuring on the 14th and 25th August, the amplitudes bearing an inverse relationship to the size of the insect. The histograms given in Figures 5a to 6a represent ln. catch values, overlayed with the interpolated values (solid lines), calculated from a model developed in this section.

Surprisingly, initial calculations had indicated that a better relationship existed for total nightly catch of a single species correlated against the mean nightly temperature, measured from 20.00 to 08.00 BST than for any other temperature measurement, such as mean nightly temperature between 21.30 and 22.30 (the period of highest trap catch for many species). As Table 1a shows, there were six temperature categories on a diurnal basis, and all of these were positively correlated with trap catch for all the species studied. This is of course not unexpected, since any temperature measurement is usually coupled to any other on a 24 hour basis. Table 2 provides the regression coefficient r, and corresponding probability levels for the five major species when a single variable logarithmic fit is performed using mean nightly temperatures. As with all single variable expressions, the dependency is obscured by the interplay of other factors, and in this instance the influence of windspeed is of crucial importance.

TABLE 2

Ln. Catch v. Temperature (^{o}C)

Species	a	b	r	r^2	p
A. tristella	-0.664	0.259	0.412	0.170	<0.1
M. secalis	-0.314	0.211	0.415	0.172	<0.1
N. janthina	1.05	0.099	0.276	0.076	>0.1
N. comes	-1.78	0.236	0.597	0.356	<0.01
N. pronuba	-0.144	0.185	0.370	0.137	>0.1

TABLE 3

Ln. Catch v. Windspeed (m/s)

Species	a	b	r	r^2	p
A. tristella	4.14	-1.07	0.656	0.430	<0.01
M. secalis	3.66	-0.912	0.692	0.479	<0.02
N. janthina	3.00	-0.487	0.520	0.270	<0.05
N. comes	2.08	-0.591	0.576	0.332	<0.01
N. pronuba	3.46	-0.885	0.680	0.462	<0.002

TABLE 4

Ln. Catch v. Temperature and Windspeed

Species	a	b_1	b_2	r	r^2	p
A. tristella	0.019	0.307	-0.966	0.964	0.930	<0.001
M. secalis	0.021	0.271	-0.881	0.973	0.947	<0.001
N. janthina	0.033	0.217	-0.362	0.970	0.940	<0.001
N. comes	-0.015	0.163	-0.606	0.952	0.907	<0.001
N. pronuba	0.023	0.255	-0.780	0.966	0.933	<0.001

All of the catch histograms show that on the night of the 19th August, the trap caught nothing with the exception of two from N. janthina (these were caught sometime between 22.00 and 22.30, when the windspeed dropped to its lowest level - albeit fractionally - when considering the period between 21.00 and 02.00). Examination of Table 3, which again contains the results from a single variable logarithmic fit between catch numbers and windspeed, shows that a much stronger association exists in this case, as compared with temperature (the mean r^2 value is 0.39 in contrast to 0.18).

Relative humidity is a rather enigmatic environmental factor in its relation to light-trap catch, exerting a small but definite effect on insect activity. Williams (1940) believed that humidity was not responsible for any independent influence, but was positively correlated with catch on warm nights and negatively correlated with cold nights, due to the combined physiological problems of retaining (a) water and (b) body heat. Harling (1968) found no demonstrable effect on noctuid and geometrid catch. Both of these studies were conducted in Britain, but other similar research conducted overseas, by Jarfas and Viola (1981) in Hungary for instance, suggested that the relevance of humidity was "ambiguous". In the present work, relative humidity as an independent variable could not be shown to have any conclusive influence, since for certain species it was positively associated with catch and in other species negatively so, but in all cases these were never significant and were almost certainly due to the random assortment of the variables.

Barometric pressure was always positively related to catch. Upon reflection, this was not an unexpected result since this factor is usually positively linked to air temperature in the summer months, and often in the early autumn (although clear nights in winter cause the reverse to be true for this season).

Although ambient illumination was monitored at half hourly intervals from 20.30 to 03.30 BST, it is difficult to analyse statistically its association with flight periodicities. It is probable that Lepidoptera possess a threshold response to light intensity, and once it has fallen below a certain level, take-off in large numbers occurs. Thereafter, aerial density is relatively unaffected by any further decrease in intensity (hence take-off times are linked to sunset times). This is suggested when Figure 6b is compared to the nightly catch periodicities of the five species studied (Figures 7a to 8a). All of these figures give averaged values taken over 19 nights.

A full account will be given in Chapter 4 of the research that has been conducted in the past into the effect of moon-phase on light-trap catches. Many researchers find that the high light levels during full moon depresses the catch, but this is by no means universal. In this study, the moon was full on the 14th August - when the trap caught the highest number of A. tristella, and second highest number of M. secalis. In fact this night saw the second largest catch of all species combined, over the three week period, during which the highest nightly mean temperature and lowest mean nightly windspeed were recorded.

The results from the first two stages of analysis indicated that the most important meteorological factors affecting catch were mean nightly temperature and windspeed. Table 4 gives the results obtained from combining these factors into a single equation thus:

$$\ln(\text{catch}) = a + b_1(t) + b_2(w)$$

(The addition of one to the catch is taken as implicit).

It is clear that, over the period of study, these two parameters only could account for over 90% of the variance associated with the ln.catch, and it is quite likely that had

the sample been larger, the accuracy would have been greater. N. comes, for instances was the species caught in the lowest numbers (see Figure 4d), and the r^2 is 0.91 as compared to M. secalis, which was caught in far higher numbers and has an r^2 of 0.95. Although it would have been a simple task to include other variables in this equation (since the process was computerised), such as barometric pressure and humidity, this was not done because the mechanisms of their operation are not well understood.

1.7. Interpretation of the b_1 and b_2 Coefficients

As the size of an organism increases, the bodily surface area increases as the square of the linear dimension, but the volume (and therefore weight), increases as the cube power. Hence the smaller the organism, the greater the rate of heat dissipation. In environments where code is a limiting climatic factor, the smaller organisms will have a greater sensitivity (expressed as behaviour) to this condition. The b_1 coefficient essentially defines this sensitivity of the five lepidopterous species to changes in air temperature, as reflected by trap catch. Because they have a range of sizes, (see page 16), it might be expected from the above discussion that the magnitude of this coefficient would be inversely related to the size of the insect. Inspection of Table 4 shows that, for the first four species (which are arranged in order of increasing size), the coefficient does indeed decline. With N. pronuba however, which is considerably larger than even N. comes, the b_1 value is 0.255, i.e. the catch rate doubles for every 2.7°C rise in temperature. This is close to the value obtained for M. secalis (2.5°C), the second smallest species in this study. It is not surprising therefore, that if

a fit is performed for b_1 against tip-to-root winglenth (mm) for the five species, the equation:

$$b_1 = 0.34 - 0.0056 \text{ (winglength)}$$

returns a p value greater than 0.1 ($r^2 = 0.027$).

The poor correlation is even more apparent in Table 2, and hence no trend in temperature sensitivity was evident within the restricted size ranges.

The b_2 coefficient, which describes the sensitivity of species catch to windspeed, is much more difficult to interpret correctly. In Britain, especially in the late summer and autumn, the only important aspect of air temperature is that of heat loss from the insect. Theother effect - water loss - does not start to limit moth flight until the temperature exceeds 20°C. A moth's airspeed, however, exerts several simultaneous influences. Both air resistance and cooling effects increase in linear proportion to area of exposure, but the force acting on a body is proportional to the square of its velocity relative to the air. Larger insects retain an advantage over smaller ones when considering resistance and wind chill, and thus larger animals make use of this by flying at greater speeds. Although, over a wide size range (10:1), the power-to-mass ratio declines as the body dimensions increase (the force of a muscle is related to its cross-sectional area and not to its mass), over a small range (as in this instance), this relationship cannot be demonstrated. Many of the Noctuidae, for instance, have faster wingbeat rates than the smaller Pyralidae. A further complication arises if wing loading is also taken into account (the ratio between wing area and insect weight), where, roughly speaking, weight is proportional to the 1.5th power of the wing area (Greenewalt,

1960). If moths were to be affected only by the physical influences of the wind, the b_2 coefficient would be directly related to insect size. Referring back to the b values obtained in Table 3, it is clear that more than just physical influence is involved since there is no readily identifiable pattern. Taking the b_2 values from Table 4, the fit between this coefficient and wing length becomes

$$b_2 = 0.96 - 0.014(\text{wing length}),$$

where $r = 0.31$ and $p>0.1$.

Furthermore, unlike temperature, windspeed does not effect aerial density in a straightforward manner, especially for migratory species. This will add to the uncertainty of the b_2/winglength relationship, since the change in the catch rate in different windspeeds is not simply a function of airborne moths. Altered airspeeds, ease of manoeuvrability and possible changes in flight altitude add to the confusion, and two additional field seasons were required before these issues were partially understood.

1.8. Applications of the General Equation

The equation

$$\ln(\text{catch}) = a + b_1v_1 \ldots\ldots + b_nv_n,$$

can be thought of as comprising two distinct parts; the first, the intercept a, is for any species dependent upon the background population and will consequently fluctuate from year to year. Conversely, the components b_1v_1 throught to b_nv_n, where v is some environmental variable, are independent of the population size since they describe the form of the relationship. The regression coefficients, b, give the rates of variation in catch about the mean level during a given time period within a species annual flight season.

dimensions but living in different climatic conditions will have the same b values, since other factors such as flight temperature thresholds will be different. Although it has not been tested, these coefficients are almost certainly limited by spatial variance.

As a predictive model it is a considerable improvement over the other single variable equations above, but inaccuracies will always arise since light-traps can only sample populations indirectly.

1.9. Nightly Catch Periodicity

Figures 7a through to 8a show how the trap catch for each species changed on a half hourly basis, expressed as a percentage of the total caught per night. The relationship between temperature (Figure 6b) and half hourly trap catch was of considerable interest, since it could be used to examine the credibility of the previous conclusions. For the microlepidoptera, trap catch is highest in the early evening between 21.00 and 22.00, and thereafter falls rapidly. The catch periodicity is quite different for M. secalis, which is presumably less dependent upon the warmer early evening temperatures; although the peak catch occurs at 22.00 BST, the level varies little until 02.00. Both N. janthina and N comes were caught in greatest numbers at 22.30, whilst N. pronuba peaked at 22.00 and 24.00. It would be wise, however, not to place too great an emphasis on this trend. As with the b_1/size analysis, no striking patterns emerge and the form of these histograms do not appear to be closely related to insect size. Temperature sensitivity alone will not account for the form of the periodicity; merely because a species has the capacity to fly at a certain temperature does not necessarily mean it will do so.

Because the atmosphere is often less turbulent during the night, windspeeds were far more constant during this time (Figure 6b). It is likely that the only effect that air movement has on the pattern of activity over a single night is to control its amplitude but not the form of the distribution.

1.10. Discussion

The logarithmic relationship that trap catch bears to temperature has been demonstrated by a number of researchers. Although Williams (1940) worked with total numbers of insects caught and not individual species, he found that the catch doubled for every 2.8°C change in minimum temperature, or 3.9°C change in maximum temperature (on a diurnal basis). With the species studied in Cranfield in 1981, the mean nightly temperature increase which resulted in a doubling of the catch, ranged from 4.3°C for N. comes, to 2.3°C. for A. tristella. The overall mean numbers resulted in a doubling every 2.9°C., which is fairly close to the value Williams would probably have found had he been dealing with mean nightly temperatures. Because Williams found a difference in the effects of maximum and minimum temperatures, it implies that eventually an optimum temperature is reached in which numbers of airborne moths remain at a constant value. Such a limiting threshold is rarely encountered in Britain - certainly the highest mean nightly temperature recorded during the three weeks, on the 14th August, was 17.4°C. Harling (1968) estimated that for both British noctuids and geometrids, log. catch is linearly related to temperature over the range 10.5°C. to 19°C. His results are of relevance to this study since both were performed in the autumn using identical equipment. Unfortunately his work did not extend to a statistical examination of individual species, and so it is not possible to test the validity of the temporal invariance of the b relationship for other British species.

The effect of windspeed upon the capture of non-mass migratory species is invariably found to be negatively related when above some threshold value. It is not possible to directly compare the results of the 1981 analysis to those of Williams in thiscase, since his scale involved six approximately logarithmically-sized class intervals between 0 and 9m/s. Furthermore, readings were taken at a height of 21.3m and were not subsequently corrected for altitude. In 1981, the data generally showed that catch was halved for every 0.96m/s increase in windspeed. Almost certainly, this value will change considerably for different species and different environmental conditions. Morton et al. (1981) for instance, demonstrated the existence of two wind thresholds. Once the first had been reached, catch started to decline. The second caused a complete cut-off; for H. armigera and H. punctiger, the lower threshold was 1.7m/s, but for the codling moth this was only 0.83m/s. The cut-off point in both cases was 3.9m/s.

As a monitoring instrument of aerial density, light-traps are working with the greatest disadvantage in windy conditions. With pheromone traps catch may be three to five times as great in slightly breezy conditions than in still air for a given species, yet a light-trap may record a slight decrease in the numbers caught per unit time (Skuhravy and Zumar, 1981). Whilst it is certainly true that a pheromone trap will not accurately represent the aerial density in calm conditions due to the inability of the males to follow pheromone trails, evidence suggests that the increase in catch is not merely an artifact to which light-traps are immune. Migratory species especially may make use of windy conditions.

Without a knowledge of the sampling efficiency of light-traps, it is impossible to estimate the size of the background population. This is of no consequence when analysing catch periodicity changes, which only depend upon the overall population for their amplitude.

N. pronuba and N. janthina display considerable similarity between their flight periodicities, the correction of which gives an r of 0.74, with $p<0.01$ (see Scattergram of Figure 8b). Flight periodicity analysis may therefore have a role as an identification aid, although it would have a strictly limited value. Certain closely related species might equally have widely diverging behavioural patterns to avoid confusion during courtship and to optimise the use of environmental resources.

The emphasis of the 1981 data analysis was towards the behavioural aspects involved with the operation of light-traps rather than straightforward population modelling. However, the examination simply of trap and weather data is ultimately limited as the reasons for their operation remain in obscurity, no matter how subtle the interpretation. At a certain stage logical deduction is an insufficient tool to establish any further progress and a recourse must be made to the judicious use of technology. Over the next two years the environmental monitoring facilities of the Group were employed to study the behavioural changes shown by moths in response to light.

CHAPTER TWO

EXPERIMENTAL DESIGN AND DATA RECORDING (1982 Fieldwork)

2.1. Introduction

The analysis of the 1981 fieldwork data demonstrates quite clearly that trap effectiveness was closely related to prevailing meteorological conditions, yet there still remained a number of unanswered questions as to the nature of operation of a light-trap; indeed, as stated in the introduction, much work has already been done and is still continuing regarding the influence of temperature, air movement, humidity and ambient light upon catch patterns of various species, but little progress has been made towards an understanding of Lepidopteran behavioural change when exposed to types of illumination not normally encountered in natural circumstances.

On the basis of this reasoning, two major areas were identified which required investigation, and which could, using EPRG imaging and monitoring technology, be quantified with some degree of accuracy. These areas were as follows:

a) behavioural changes elicited by a light source upon the flight pattern of a moth;

b) an absolute measure of trap efficiency (some form of calibration), relating catch against local moth aerial density or flux.

It is important to note that neither of these objectives can be realised by merely operating a light-trap, however dedicated and thorough the experimenter, without some additional form of monitoring.

The first of these objectives, concentrating upon behavioural change, was the major topic of the 1982 fieldwork, and the data collected proved to be so prolific that three chapters are concerned with its collection, analysis and interpretation.

2.2. Choice of Monitoring Period and Location

The work of 1981 had been carried out from the 10th to the 30th August, and although the emphasis of the 1982 work was behavioural analysis and not investigation of weather factors, it was decided that for comparison between the two years, both the time and location should overlap. Hence this field season commenced on 26th July and finished on 11th September; the finishing date, unlike that of the previous year, was not decided in advance but only after it was felt that sufficient data had been gathered. Again, the species of interest were those that had already been on the wing for some distance, and had not merely emerged from any local vegetation. Light sources were therefore placed as shown in Figure 2, away from any substantial cover - indeed after the wheat field had been harvested and the stubble burnt on the 28th July, the only substantial cover was at least 150m distant.

2.3. Experimental Objectives

The purpose of the fieldwork conducted in 1982 was the observation and recording of night flying moths exposed to various types of illumination. Because they fly at night, it is not possible to simply film or video record them - low light levels demand some increased sensitivity on the part of the monitoring system. To enable the reception of low intensity signals, it is necessary that they are amplified before being processed by standard T.V. apparatus.

2.4. Equipment and Experimental Configurations

a) The Imaging System

The video amplification was provided by a Modulux image intensifier (I.I.T.) coupled to a Sony T.V. camera. As a crude analogy, image intensifiers work upon light in a similar manner as an audio amplifier works upon sound; any signal received is greatly magnified and allows the user of such a device to see in the dark, with the minimum of illumination. The active device within the Modulux casing is an English Electric Valve Intensifier Tube (EEV-P8076DC), having a luminance gain of approximately 10^5. The sensitivity of the intensifier peaks at 520nm whereas the re-radiation from the earth at night is similar to that from a black body at 290K, reaching a maximum at 10μm. Virtually no radiation is present to which the intensifier can respond (which would represent interference), and the necessary illumination of the moth targets was provided by the lamps to which their behaviour was orientated, namely a quartz-halogen tungsten lamp focused as a beam and a 125W MV lamp. The emission spectra from both of these sources are given by Figure A4.
The intensifier also offers low distortion of images over the visual field (6%), although this can only be achieved at the expense of uniform gain over this area; thus gain increases towards the centre of the output screen, but since all moths viewed returned a signal well above the critical threshold brightness, this was not a significant disadvantage. An automatic gain control (agc) circuit provides a constant output with respect to the total (integrated) energy, regardless of the strength of the incoming signal.

b) Narrow Beam Source

Earlier in 1982 it had been decided that an important facet of this field of research was changes which occurred in the flight of a moth when it is suddenly exposed to a bright source of light from a region of relative dark, such as a "normal" night sky. This required the source to have a clearly defined beam shape, and for this reason a parabolic reflector such as used in search lights or torches was unacceptable (because of the side-lobes; see Appendix A). In addition, it was essential that the angular width of the beam and so intensity could be easily altered, as well as changing the emission frequency by the use of suitable filters.

The final design of the source is illustrated in Figure A3 and Plate 1 , with the top panel removed. The light from a tungsten quartz-halogen lamp is collected by means of a condensing lens L1, and is then focused into the desired beam shape by the series of lenses L2 to L4. L3 in this series is mounted upon a motorised worm drive which allows the beam angular width to be altered from a minimum of 4^{o} to a maximum of 28^{o} by the use of an external switch (during the field work however, the maximum angle used was 25^{o}). A slot in the top panel enables the insertion of any desired filter.

This light source was then mounted on a moveable frame allowing it to be positioned at any compass bearing, as well as through any angle of elevation from -20^{o} to $+20^{o}$ from the horizontal. At this stage it was uncertain whether or not the device would attract any insects (which would presumably fly down the beam), and so a suction tube was added to the end of the casing, in which a pair of optical sensors were mounted to register the passage of any object. Figure A3 shows the completed device.

The presence of an agc circuit on the intensifier required that considerable care was taken with the orientation of the equipment. Although it was quite capable of detecting signals far below that of the human visual threshold, because the light reflected from a moth at 20m is feeble in comparison to that of a street lamp even at 1Km, it was essential that fieldwork was performed where there was a minimum of background competitive illumination. Practical trials revealed that since the camera was to be used horizontally for some experiments, the only part of the horizon which was satisfactory was at a compass orientation between 1^{o} and 20^{o}, i.e. approximately North. The light source was to be used in a number of orientations, but always with the camera pointing in the direction indicated by Figure 9. Table 5 provides information on the various orientations used for both camera and beam, together with elevations and associated dates. A pilot survey revealed that when the camera was in line with the beam, i.e. sighting along it, best results were obtained using a lens of 200mm focal length and the source about 17m away from the camera. When the beam was at 90^{o} to the camera, a wider field of view was required and so a 35mm focal length lens was used; Figure 9 shows the positioning of the equipment.

c) Elevated 125W MV Robinson Trap

Interesting though lepidopteran response to a sudden light exposure is, most light-traps do not emit a closely defined beam. Standard traps usually illuminate a far greater angular volume (2π rad for a Robinson trap placed at ground level), and so moths will perceive the light from a greater distance, giving more time for their eyes to become light-adapted, as discussed in the introduction.

TABLE 5

Narrow Beam Monitoring Study 1982

Date	Monitoring Period (BST)	Camera Compass Bearing (Deg)	Beam Compass Bearing (Deg)	Beam Elevation (Deg)	Beam Width (Deg)	Source/ Camera Separation (m)	Lens Focal Length (mm)	Beam Filter
1/8	22.30-22.50	16	286	5	25	14.1	35	Blue
	22.50-23.10	16	286	5	25	14.1	35	Red
	23.10-23.30	16	286	5	25	14.1	35	Green
3/8	22.00-22.20	16	16	10	20	17.0	200	Blue
	22.20-22.40	16	16	10	20	17.0	200	Red
	22.40-23.00	16	16	10	20	17.0	200	Green
3/8	23.10-23.30	16	16	10	7	17.0	200	-
	23.30-23.50	16	16	10	20	17.0	200	-
	23.50-00.10	16	16	10	20	17.0	200	-

TABLE 5 (Continued)

Narrow Beam Monitoring Study, 1982

Date	Monitoring Period (BST)	Camera Compass Bearing (Deg)	Beam Compass Bearing (Deg)	Beam Elevation (Deg)	Beam Width (Deg)	Source/ Camera Separation (m)	Lens Focal Length (mm)	Beam Filter
8/8	22.00–22.20	10	280	10	20	17.3	35	-
	22.20–22.40	10	280	15	20	17.3	35	-
	22.40–23.00	10	280	5	20	17.3	35	-
11/8	21.45–22.05	20	20	7.6	15	17.3	200	-
	22.05–22.25	20	20	10	15	17.3	200	-
	22.25–22.45	20	20	15	15	17.3	200	-

Casual observations of moths flying around a Robinson trap during 1981 indicated that they tend to fly within ± 30cm of the horizontal plane of the lamp, and so a camera positioned to receive a plan-view image of this plan would, if placed at a suitable distance, enable a reliable estimate of moth ground speeds.

Initially it was intended to mount a camera above such a trap positioned at ground level, but a number of objections made this impracticable. Firstly the camera and intensifier had to be at least 4m in the air, pointing downwards or with a suitable mirror system, but because of the weight (11.2Kg), a gantry could not be constructed in enough time to provide an absolutely stable platform (it is worth remembering that even a slight oscillation of a camera results in a highly unstable image). Furthermore, light reflected off the gantry would doubtless have influenced moth flight behaviour. Lastly, because the lamp would be in direct view of the intensifier, a matt black baffle would need to be placed over the bulb. In fact, even this precaution would be insufficient due to reflections off the ground and surrounding vegetation. The resulting diameter of such a baffle (at least 2m) would have completely masked the area of interest, as well as radically altering the specifications of the trap.

The only part of a Robinson trap of significance to catch is the conical centre section bearing the bulb and vertical baffles, into which moths fly and subsequently drop into the basin below; this is silvered and reflects any light falling on it. No light however falls on the basin (which is black in any case) or the collar, due to the geometry of design. Instead then of mounting a camera on a mast, this part of the trap, which had a modified base to accept a collecting bottle, was

secured by means of a horizontal metal arm of length 50cm to a Clark pneumatic mast in such a manner that no light was cast upon the mast or surrounding equipment. Once the trap is raised off the ground, the angle through which light is cast increases from 2π to 2.35π radians, before striking the ground, as shown by the inset of Figure 10.

The camera and intensifier were positioned horizontally at the base of the mast, with a mirror angled at 45^{o} enabling the camera to receive an image of the light-trap in plan view.

Two sample heights were used, one at 5.0m and one at 7.1m. In order to obtain as wide a field of view as possible around the light, a 17mm focal length wide angle lens was coupled to the intensifier. On the rectangular monitor screen, this gave a view angle of 36.6^{o} from left to right and 28^{o} from top to bottom. To facilitate data interpretation, the camera and mast were always arranged so that the top of the screen was towards magnetic North. Figure 10 shows the fieldwork configuration as just described, and equipment settings are given in Table 6.

d) Wind Measurements

The narrow beam study involving sudden light exposure suffered from a serious disadvantage - the depth of field was so great when sighting along the beam that no detailed quantitative analysis of the effect of wind could be made. As a consequence, it was not necessary to know the instantaneous windspeed close to any particular moth. For wind measurements then, a Porton cup-and-vane anemometer, which outputs speed and direction as analogue voltages, was found to be perfectly adequate. The information was fed to a dual trace Toa chart recorder, as well as to a Racal

TABLE 6

Elevated Robinson Trap Monitoring Study 1982

Date	Monitoring Period (BST)	Trap Height (m)	Lens Focal Length (mm)
6/9	20.45-21.45	5.0	17
8/9	20.45-21.45	5.0	17
9/9	21.00-22.00	7.1	17
10/9	21.00-22.00	7.1	17
11/9	21.00-22.00	7.1	17

Store-4 FM tape recorder.

This equipment alone was not accurate enough to be used in conjunction with the Robinson trap/video study. Here it was essential to know instantaneous speeds, which called for a fast response time on the part of the probes. Thus a set of Lowne vane anemometers were used (Type RH2), modified by EPRG for digital readout. These instruments can be used in speeds up to 15m/s, and have a threshold response of 0.11m/s. In addition, the anemometer has a wind directional cosine response accurate to 0.5% for a 10^{o} off-axis flow, increasing to 1.5% for non-axial flow in the range 50^{o}-70^{o} (Scannell, 1983).

With the imaging system described, it is clear that only movement in the horizontal plane could be recorded and it was therefore not necessary or relevant to record vertical air movement. Two vane anemometers, one orientated with its axis N/S and one W/E were attached to the mast, 2.73m below the lamp of the trap for all cases. The outputs from these were connected to the spare channels of the Racal Store-4, since the Porton was still used to measure windspeed and direction.

e) Measurement of Time

To record elapsed time (each night's run was normally to last for one hour), a second camera was focused upon a digital clock and its signal mixed with the first by means of a signal mixer and Sony sync generator. The monitor screen thus displayed both the view from the intensifier plus the time, to 1 second resolution, at the bottom of the picture. Since the data was video recorded, the progress of any moth could be followed every 0.002 seconds (the video system operated at a 50Hz field rate and a framing rate of 25Hz - see Appendix B).

f) Measurement of Illumination

Monitoring did not always commence at the same time on each night (see Table 5), but only after the ambient illumination had fallen below a threshold of 1.0 Lux. This was measured by a photoresistor mounted at the focal point of a 16cm parabolic reflector, positioned vertically on the roof of the field hut, and connected to a multimeter.

2.5. Practical Implementations of the Narrow Beam and Robinson Trap Monitoring Systems

No major practical difficulties were encountered using the narrow beam system, but as previously stated, this yielded information which though valuable, could only be qualitatively assessed. The fundamental problem here was the small amount of airspace being illuminated - for an angle of 10^{o}, this is only o.4% of the volume given by a Robinson trap placed at ground level. For those experiments where the camera was placed at 90^{o} to the beam source, the length of the beam which could be viewed on the screen was only 4.8m. Consequently, the sample volume at beam spreads of 7^{o}, 10^{o} and 15^{o} was a mere 0.38, 0.78 and 1.77m^{3}. The number of moths entering this volume, even on a clear night, was not more than 50 per hour, and any that did enter stayed for only a fraction of a second. Although this data was collected within a closely defined volume and might have been used as a basis for calibration, the visibility of the beam modified the behaviour of the moths which entered it, making any such calculations unreliable. To increase the volume sampled, there were two possible alternatives:

a) move the camera further from the beam;

b) sight the camera along the beam.

The first of these was considered but then decided against; the camera was already 17.3m from the mid-point of the beam (as seen on the screen), and at 90^{o} to the camera the light was side-scattered and therefore less efficiently used. This became a serious problem especially at distances greater than 15m along the beam where the intensity was greatly attenuated. The second alternative retained a number of advantages over the first; firstly, since the camera would be directly behind the beam (at a distance of 17m), light would enter the intensifier by means of back-scattering, viewing moths at a much greater distance. In addition, without increasing the distance of the camera from the source, a much greater volume was being sampled by effectively increasing the depth of field. Unfortunately, this last benefit contained an inherent drawback as it was now impossible to estimate with any confidence the distance of a moth from the camera, and therefore its ground and airspeed. Other than describing the pattern of flight which occurred when entering the beam, the only other piece of information which could be gleaned from this fieldwork was calculations of wingbeat frequencies.

The vertical viewing system incorporating the Robinson trap proved to be highly successful, both with regard to ease of implementation and quality of data obtained. It was first used on the 6th September and performed adequately, but on the night of the 7th the low night temperature caused the mirror and 17mm lens to continually mist over, resulting in the loss of one night's data. To prevent such a repetition, a heating element was constructed from steel wire and attached to the underside of the mirror, drawing 0.3A at 12V. This raised the temperature of both mirror and lens sufficiently above the ambient for them to remain clear.

Using the Robinson trap, orientation (other than choice of site) was irrelevant since the light emitted is cast through 360°, so the only major consideration was where to place it. The limiting factor in this case was the length of cabling available for power supplies and data channels, and so once the site had been chosen, it was not changed from night to night (see Figure 2).

2.6. Transfer of Data to Computer

Figure 11 depicts, in block diagram form, the recording and display devices of the complete data collection system. The quantity of data collected was so large that analysis by hand would have been immensely tedious and prone to innumerable errors. This data comprised two categories:

1) moth flight trajectories, as recorded by the camera;

2) wind information, both digital (DVA system) and analogue (Porton).

a) Transfer of Moth Trajectories

Since the recording system used standard video technology, each video field was separated in time by 20ms; frozen images of a moth's progress were therefore produced every 1/50th of a second. Now a monitor (or T.V.) screen can be thought of as a rectangular area, any point upon it bearing a unique x and y co-ordinate value. The problem was to translate the co-ordinates for each moth track into a form acceptable to the computer. This could of course be done by hand - by placing a grid of suitable dimensions upon the screen and then noting the position of the head of the moth track frame by frame, for each moth. This would have been laborious in the extreme.

In his thesis "The immediate extraction and display of insect flight trajectories from infra-red signals", Bent (1982) describes an automatic system which takes live T.V. signals and converts each field of an insect's flight into two voltages relating to the x and y position on the screen. It is important to note that in this case, the intensifier, although still operating at 50Hz, was electronically shuttered and only active for a maximum of 30 microseconds for every 20 milliseconds. During this period, a 60KW pulsed xenon discharge searchlight would fire, giving a very high signal to noise ratio. Insects would be seen as bright points of light against a virtually black screen, even at midday, and so the circuitry had little difficulty in discriminating between noise and data (Schaefer and Bent, 1984).

In such a pulsed mode, however, streaked-images are not produced on the monitor screen. For this to be possible, the intensifier must be operated continuously. In this manner, although a new image is still formed every 1/50th of a second, a track which moves for example 2cm on the screen in that time will be displayed as a streak and not as a point, due to the decay characteristics of the intensifier phosphor output screen. This makes possible such measurements as wingbeat frequencies, which are displayed as intensity modulated streaks. The disadvantage of this mode of operation is that it is impossible for the automatic circuitry to accurately identify the head of the track. Also, this processing cannot be performed with recorded data, since the background illumination levels are found to be prohibitive.

What was needed was some form of "lightpen", strictly speaking a light-sensitive pen, which when pointed at the screen, would produce two voltages corresponding to the x and y co-ordinates of that point. The detailed construction

of this device appears in Appendix B. It had to be similar in principle to standard computer lightpens, but in this case the screen pointed to was not part of the computer system. Furthermore, a greater degree of precision was required as the pen had to distinguish quite discrete points and not a general area.

Once the pen had been built, it was interfaced to an Apple II Europlus microcomputer via an analogue to digital (A/D) converter, and the moth flight trajectories from a total of 14h of video tapes, taken over a period of 6 weeks, were transfered first to memory and then to floppy disc. This took 3 weeks, but the pace of work was quite leisurely.

Error-checking Routines

Although a large number of tracks were now resident on disc, there was still much work to be done before any analysis could be performed. The data had to be examined and spurious data points removed, these resulting from random voltage spikes in the system. After this, flight tracks had to be smoothed, since inputing data by light-pen produces tracks of a slightly irregular quality, which although insignificant when dealing with mean speeds taken over tens of points, the error increases in magnitude the smaller the time scale analysed.

The programmes which rejected errors relied upon scanning techniques to estimate the likelihood of the next point being within a radius of the point preceding it. This eliminated 90% of the random-noise errors. For smoothing an entirely different process was employed. Here a programme would take a running mean of three data points, incremented by one each time, and store the calculated value. This reduced the number of data points in a track from n to n-2 (a loss of 0.04 seconds), but this was fairly

inconsequential when considering the full length of the track. Any tracks of less than 0.1 seconds in duration were not analysed.

The bulk of the subsequent analysis was performed upon data gathered on the 6th, 8th, 9th, 10th and 11th September, and the number of viable moth flight trajectories were as follows:

6th:	105	tracks (6655 data points)
8th:	104	tracks (6537 data points)
9th:	90	tracks (6181 data points)
10th:	71	tracks (4661 data points)
11th:	50	tracks (2810 data points).

Whilst only a proportion of the available data was selected as being of sufficient quality for analysis (30%), it must be emphasised that this was a computer process and not subject to experimenter bias (due to fatigue or changing tolerance thresholds), except in the case of actually writing the criteria for rejection or acceptance into the software. Even here, any induced error would be a constant since the same rejection conditions would apply to every track. It is therefore considered that the data as stated above, was, as far as is possible, a representative sample of the whole.

Calibration of Flight Trajectories

Calibration of the stored co-ordinates was a two stage process:

a) defining the x and y voltages produced by the lightpen into equivalent computer screen units;

b) defining the computer screen units in terms of metres.

The first of these is detailed in Appendix B and shall not be dealt with here. For the second stage, it is important to note that the Apple high-resolution screen is set at 280 points along the horizontal and 192 along the vertical. As mentioned earlier, two sample heights were used, one at 5.0m and one at 7.1m. Calibration was performed by marking out a known length on a white background and demarking this with black masking tape. This was then viewed with a video camera set at 5.0 and 7.1m, in each case transferring the co-ordinates to the computer using the described system. The results were as follows:

i) at 5.0m, one screen unit is equivalent to 1.36cm, giving a view area of 3.8m along the horizontal and 2.62m along the vertical;

ii) at 7.1m, one screen unit is equivalent to 1.88cm, giving a view area of 5.26m along the horizontal and 3.61m along the vertical.

b) Transfer of Wind Information

The DVA processor outputs binary numbers, the value of which change according to windspeed. This data can be transferred at 5Hz or, as in this case, 10Hz. In zero wind, the value 128 is output. With increasing positive wind, the value changes upwards from 128 towards a maximum of 255. Similarly, wind in the reverse direction causes the processor to count down from 128 towards zero. The calibration for this device appears in an EPRG report. For a sample rate of 10Hz, the equation for

deriving the windspeed is:

$$Vt = (Nt-128)Ko.10+11$$

for positive windspeeds and

$$Vt=(Nt-128)Ko.10-11$$

for negative windspeeds,

where Vt is the wind component as found for that anemometer, Nt is the decimal equivalent of the binary number produced by the processor for that windspeed, and Ko is the slope coefficient (2.434). For Nt=128, Vt=0.

Traditionally, the output from the DVA processor has been first input to an A/D converter interfaced to the Apple computer to detect the presence or absence of digits (Bent, 1982). This is in fact unnecessary, since the computer can already accommodate serially coded digital signals, input via the "games" connector. All that is required is the construction of a simple comparator circuit to decode the combined data and synchronization signals coming from the processor (or, as in this case, the Store-4 since the data had already been recorded), raise them from 1V to 5V (to make them TTL compatible), and input them to the machine. Appendix C gives details of this circuit design and use.

To read the wind data into the computer, a suitable assembler language programme had to be written (high level languages are not feasible here due to speed restrictions). Once the data had been read, it was stored as binary information again on disc and any wind value could be recalled and displayed to a precision of 10Hz.

Porton data, unlike the above, was in analogue form and therefore had to be first processed by an A/D converter at a rate of 2Hz before storing on disc. This was a straightforward process however, and, like the above, was available for examination once stored.

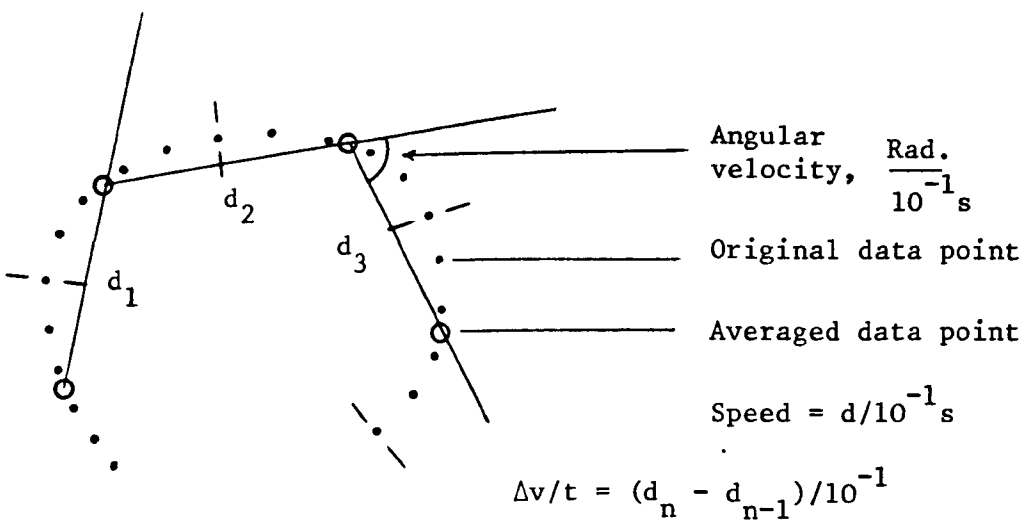
2.7. Computer Analysis of Moth Flight Trajectories and Wind Data

After data storage and calibration, it was decided that the most important aspect initially was to gain a visual impression of the tracks recorded. Two programmes were therefore written, once which plotted each moth track in a rectangular area showing the position of the light, and the other showing windspeed and direction given by the Porton and DVA probes, both averaged to 0.5 seconds, for three seconds prior to the track and for seven seconds after it had commenced. Figures 14 and 21 are sample outputs from these programmes.

Following this stage, the next programme package consisted of a control system - FLITRAP Control Programme (FCP), which loaded wind and track data from disc, and ensured the correct synchronization of the information. This was then operated upon by the Flight Track Analysis Programme (FLITRAP). For each track, this programme produced an output as shown by Figure 12. In every case, mean, minimum and maximum ground speeds were calculated (m/s), together with maximum acceleration, deceleration (m/s^2) and maximum track angular velocity (rads/s). When each of these values occured, the associated distance from the trap was calculated (m) and the position, by dividing the visual area into a 10 x 10 grid (see Figure 13). Again, for each of these values, the direction of flight was estimated (relative to compass North), and whether the moth was approaching or receding from the trap. The flight path section then calculated how long a moth remained at particular distances from the trap, in annuli 25cm wide, thus providing radial

statistics on a "preferred" radius. This procedure was also performed for the grid references. All of the above calculations were then repeated with the wind vector components subtracted from the ground speeds, to give airspeed vectors.

It is essential to note that all of the above calculations were performed by averaging over 1/10th of a second, to reduce scatter from sampling errors. The diagram below shows how this averaging process was handled by the programme.



FLITRAP was the major tool in handling raw data and providing statistics for other packages to handle. After the information from FLITRAP had been collected and processed, the next stage was to estimate where the total number of moths spent most of their time when in the viewing area. The 10 x 10 grid above did not provide sufficient detail, and so a set of scanning programmes were written which examined each data point (i.e. every 1/50th of a second) and performed the following:

i) calculation of position, in Cartesian geometry, storing the values in a 28 x 19 array;

ii) calculation of distance from light source centre;

iii) calculation of angle subtended from light source.

Programme (i) produced as its output a 3D plot with time as the z-axis and the x and y as the visual area around the trap. Programme (ii) produced a histogram for each night, for time spent in each annular area, in 5cm increments. Programme (iii) produced a second set of histograms for time spent at each radial sector (6^{o} resolution). Outputs from all the above analysis programmes are given in the next chapter.

The purpose of this chapter has not been to discuss the analysis or interpretation of the collected data, but to describe in sufficient detail the fieldwork system together with the transfer and analysis procedures to enable a second experimenter to become familiar with the methods described; practical details of running programmes and setting check procedures have been omitted since they are not strictly relevant and can if desired, be provided by EPRG.

CHAPTER THREE

THE INFLUENCE OF LIGHT ON THE FLIGHT BEHAVIOUR OF MOTHS
(1982 Data Presentation and Analysis)

3.1. Preliminary Discussion

In the introduction to this thesis there was given a brief description of the physiological changes that occur within the ommatidium of the insect compound eye when exposed to different levels of illumination. The adaptive significance of this is clear, being the same for all organisms which possess an advanced visual system; under increasing illumination the morphology of the eye alters in order to protect the pigmented retinal cells from over-stimulation and subsequent blindness.

This fact is of particular relevance to the narrow beam studies, in which moths were video-recorded as they entered a well defined volume of light from a dark night sky. Before the experiment had been performed it was thought that the beam and suction device should have caught some small percentage of a normal tungsten trap, in proportion to the volume illuminated (defined by the beam angle, which, as mentioned in the previous chapter, was 0.4% of the volume illuminated by a Robinson trap). Consideration of the above implies that since a standard trap is visible to a moth from a long distance, the eye might well have time to accommodate to the rising energy flux as it nears the source. This was not the case with the narrow beam studies, when a sudden transition would be made from dark to light (except, possibly, for the very low percentage which were in line with the beam originally). Almost all of the moths detected by this system displayed a marked escape response, and only one from about 200 that entered the beam was caught. This is in complete

accordance with standard insect behavioural theory; the insect behavioural repertoire is to a large extent pre-set and inflexible (Matthews & Matthews, 1978), and when presented with an unfamiliar or potentially harmful stimulus an escape response is evoked. The moths upon entering the beam would usually react by executing a sudden dive or, less commonly, climbing sharply (Figure 14a).

In contract with this, a large variety of track types were found when moths were seen in plan view, flying within 4m of a 125W MV Robinson light-trap as previously described (see Plates 3 to 5). Some, as shown in Figure 14b, might suddenly appear within the field of view having flown upwards through the light/dark interface (see inset of Figure 10). These would often disappear radpidly by diving downwards after a brief erratic flight lasting not more than 0.5 seconds within the region of illumination. This form of track can once again be explained as an avoidance response, and accounted for approximately 5% of the track events.

However, most of the tracks seen within the visual area exhibited a greater degree of elaboration than a mere escape reflex, and although the duration and form of these was influenced by the prevailing weather conditions, the most noticeable impression was one of disorientation. Figure 14c was one commonly occuring type, involving sinusoidal flight towards the source, often becoming more pronounced and with greater speed changes, until at some stage the moth was caught, or more usually, flew rapidly away. Helical spiralling flight (Figure 15a) occuring along the axis of movement was also observed, but flight which involved circling the lamp took place infrequently (Figure 15b). Although these Figures imply that the types of track encountered could be rigidly classified, in reality this was not the case. It is true that helical spiralling flight was the most often seen; but most tracks usually incorporated a variety of patterns, e.g. helical flight switching to sinusoidal weaving. At this stage no assumption has been made concerning the form or frequency

of the track types seen; circling of the lamp was not a common form of flight (less than 2% of all tracks), but this behaviour is very often observed with moths flying around a domestic light bulb. The pattern of flight may therefore have been influenced by the condition of the environment.

Simply by play-back of the video tapes it was possible to identify four major areas which required further quantitative analysis:

1) the number of tracks counted within a 4m radius of the trap far exceeded the numbers caught in any given time;

2) the degree of disorientation appeared to be inversely related to the distance from the light source;

3) moths were rarely seen to fly directly over the lamp;

4) the duration and number of tracks seemed to be associated with weather factors, in particular local wind vectors.

The third tentative conclusion in the above list demanded immediate investigation, as it hinted that the standard notion of photo-tropotaxis was not entirely correct when applied to night flying Lepidoptera.

3.2. Time Surface Matrices, 6.9.1982 - 11.9.1982

The scanning programme (a), mentioned at the end of Chapter 2, was written in order to establish where the video-recorded moths spent most of their time in the area around the light-trap. The visual area was divided into a 28 x 19 grid, and for each data field according to its postion, the respective grid reference, at its centre point, was incremented by one unit along the z-axis, one unit representing 1/50th of a second. This incrementation process was performed separately for each night of data (lasting 1h), since the accumulation of all data from

the 6th to the 11th would have hidden any differences in the distributions attributable to differing meteorological conditions. Figure 16 provides a plan view of the area involved. This particular configuration (28 x 19) was chosen not only because the monitor screen is rectangular, but because of compatibility with the Apple high-resolution graphics organisation. In fact, more not than 24 x 19 positions were within the monitor area. The total area seen by the monitor was either 3.27 x 2.62 metres or 4.51 x 3.61 metres, depending on whether the trap was at 5.0m or 7.1m height. Each square within this represents either 0.136sqm or 0.188sqm.

Figure 17 is the time surface matrix (TSM) for the accumulated data taken over 1h (20.45-21.45 BST) for 6.9.1982, with the trap at 5.0m height. For this hour the windspeed averaged 0.89m/s at trap height (see Table 15 for all windspeed measurements for the 6th to the 11th August), blowing from almost due south at 188.5^{o}. Figure 18 shows samples of the wind traces collected by the Porton system at various times during the hour.

Initial inspection of this plot clearly shows a non-homogeneous density structure, with the tracks tending to cluster in an area downwind from the trap. Most conspicuously, the area in the immediate vicinity of the trap is markedly depressed, revealing that little time is spent in this region. The surface can be examined in greater detail by taking transects, of a single grid square in width, at various angles across it, which are given by Figures 19a - 19d. The orientations of these are W/E, S/N, SW/NE and NW/SE respectively.

The first transect (W/E) is strongly symmetrical about the centre point (The position of the trap), with time spent at each distance interval falling off if greater or lesser than about 80cm. It must be stressed at this point that the reduction in time spent over the source was not an artifact due

to the tracks being eclipsed as they passed over the trap; linear interpolation was performed for any track that did pass over, and the "invisible" data points obtained by calculating the speed before disappearance and after re-emergence. Because of the radius of the trap (16cm) and the speed of most moths in this region, this interpolation rarely involved more than five data fields. The S/N transect is in contrast dramatically assymetrical about the mid-position; little time is spent on the upwind (southern) side of the trap, again falling when immediately over the source and then rising sharply to a maximum of 1.18 seconds at a distance of 70cm from the trap. This transect clearly demonstrates the important effect that wind has on the density distribution in the immediate area of the trap.

The SW/NE transect also shows to some extent the above distribution, but in this case the assymetry is slightly less apparent since the transect is taken at 45^{o} to the flow of the wind. Similarly, the NW/SE reflects this pattern but in this example the distribution is rotated through 90^{o}. Thus a combination of the last two transects provides a symmetrical density distribution, similar to that given by the W/E transect.

On the evening of the 8th September, data was collected again between 20.45-21.45 BST, with the wind having veered by 45^{o}, blowing from 220.2^{o} at a speed of 0.84m/s at trap height for the duration of the sample period (see Figure 21). The trap was again at 5.0m. The TSM for the data (Figure 20) reveals a density distribution rotated through 45^{o} corresponding to the change in direction of wind flow. The build-up takes place in the North-East quadrant of the surface, downwind from the trap. Once more the area immediately around the trap is characteristically depressed, despite some time being spent in the upwind quadrant. The SW/NE transect (Figure 22) is taken parallel to the flow of the wind, reading from left to

right, and clearly indicates a density peak in the downwind region. The other transects demonstrate the effect of wind on the density distribution in accordance with their angles relative to the flow, with the NW/SE transect as the one symmetrical plot.

Before examining the data collected for the 9th, 10th and 11th September (when the trap was placed at 7.1m height and the wind was considerably stronger), it would be useful to make a qualitative comparison of the nights so far presented. Apart from the shift in wind direction, the mean windspeeds were virtually identical and the resulting TSMs show a startling degree of congruency. In the next chapter a more quantitative assessment will be made of the reasons for finding these distributions, but now it is intriguing to note that the speed at which the wind influences the distribution is well below the cut-off point for trap catch, indeed well below the maximum airspeed of most Lepidoptera. Moreover, the density depression which occurs around the trap, becoming especially apparent at a radius less than 40cm is not an effect of the meteorological conditions; it continues outwards in both upwind and downwind directions.

On the night of 9th September, when work took place between 21.00-22.00 BST, the wind direction had not changed (219.6°), although it was now considerably stronger, averaging 1.7m/s over the hour (Figure 24). The TSM of Figure 23 is little different in essence from that of the previous night, although the higher windspeed reduced the number of track-events detected by the imaging system. This became especially obvious on the 11th September, when the mean windspeed was 2.66m/s.

As the windspeed rises, the distribution changes accordingly until, at above 1.7,/s, very little time is spent in the area upwind of the trap - the TSMs of the 10th and 11th (Figures 26 and 29) clearly demonstrate this, when the wind was blowing

from 235.7° and 115.4° respectively. What is of interest in the data contained in these last two nights is the certain shift in the distributions in connection with the change in wind direction. The W/E transects for the 10th might almost be a mirror image for the same transect of the 11th (Figures 28a and 31a).

The TSMs and associated transects were an important visual aid during the initial stages of analysis and in the later stages when constructing a working behavioural hypothesis. They indicated that track density did not increase to a maximum at the source epicentre, but peaked at a distance of about 40cm. Although the amplitude of the peak was related to wind flow, being greater in the area downwind from the lamp, the same peak, with a reduced scale, occured in the upwind regions. Thus in absolutely calm conditions a radially symmetrical "doughnut" distribution might be expected. This phenomenon was studied in greater detail in the next section.

3.3. The Calculation of Radial Density Distributions

To specify the manner in which the overall density changes with changing distance from the trap (regardless of angular position), the second scanning programme described at the end of Chapter Two analysed each data field and, according to the distance from the trap calculated for each track point, built up a nightly histogram representing time spent in each annular area as depicted in Figure 16. Each annulus has a width of 5cm, and so the area of each annulus increases proportionally. On a null hypothesis, it should be expected that the time spent in each annulus is similarly proportional to the area; this distribution should occur if the calculations were based on a series of inert objects appearing with uniform randomness inside the visual field. The scanning programme in effect summed the total number of events in each annulus for

each hour, where Figure 32a is the histogram obtained from this programme for the 6th September. Although the histogram at first sight seems to be a close approximation of some theoretical normal distribution with $\bar{x}$ = 92.62cm and σ = 37.11cm (overlayed curve), with in addition a set of overlapping populations having displaced means, to obtain a true assessment of the way in which density changes with distance it is necessary to correct for the area of each annulus. The total time in every annulus must therefore be divided by the respective area to arrive at the density, i.e.

$$\frac{\Sigma \text{ no. events in each annulus/hour,}}{\pi(r_2^2 - r_1^2)} \qquad (1)$$

where $\pi(r_2^2 - r_1^2)$ gives the area of the annulus.
Figure 32b may be thought of as a TSM collapsed into a plane, this being for 6.9.1982. The density rises sharply to a peak between 40-50cm away from the trap, and thereafter decays gradually until almost zero at a radius of 2m. For the 8th, when the meteorological conditions were very similar, the density distribution (Figure 33a) is almost identical with a sharp rise and slow decay characteristic.

As the speed of the wind rises, this kind of regular distribution becomes less well defined, as shown in Figures 33b to 33d (9th, 10th and 11th). Though the density still peaks between 40-50cm away from the trap, the tail-off is now more gradual, and approximates a plateau for up to 1.5m distance. This is almost certainly due to the wind having a critical effect on the flight capability of the airborne moths. This last consideration is very significant, since it implies that whilst the area in which moths spend most of their time around a light-trap is strongly influenced even by light winds (i.e. the TSMs of the 6th and 8th), the density distribution with respect to distance changes little until the wind is above a certain threshold. The radial density distributions for the 6th and 8th are likely to remain

relatively unaltered even in absolutely calm conditions, enabling the formulation of an hypothesis describing the ideal area distribution in still air.

3.4. An Analysis of Dynamic Flight Strategy

The programme FLITRAP enabled a highly detailed examination of each track event detected by the imaging system, and the sample output of Figure 12 is one of 420 similar print-outs, with each flight parameter calculated to a resolution of 0.1 seconds.

When dealing with bodies in flight there are always two stages in dynamic analysis, since the medium is rarely completely calm. Thus an aircraft (for instance) has a groundspeed which may be defined as the distance covered per unit time relative to the ground, and an airspeed, which is its groundspeed having subtracted vectorally the speed of the moving air around it. In terms of energetics, it is the latter consideration which is of greatest importance as only this provides a true measure of the work done in staying aloft and moving through the medium. The dual nature of this problem becomes much more acute with animals that are able to fly, since it may be completely incorrect in certain cases to subtract the wind vector and state "there - that is what the animal would have done if the air had been calm". Flying creatures often incorporate the prevailing meteorological conditions into their overall flight plan, becoming an integral and inseparable part of what may now be termed their dynamic flight strategy.

For most insects and especially the Lepidoptera, maximum airspeed is low when compared to the windspeeds which commonly occur in Britain, and so the problem is made yet more complex when one considers that if the windspeed is considerably greater than the maximum airspeed of a moth, dynamic flight strategy may be completely masked since the animal is bound ultimately

to be dominated by the flow of the wind.
The effect of wind is therefore rather intricate and will be dealt with independently in a later section. In this section, analysis will be made of the observed behavioural changes, and since these include not only groundspeeds but also other variables such as accelerations and approach attitudes, they may be called absolute parameters.

Having found the mean, minimum and maximum groundspeeds for each moth on the 6th to 11th September, Table 7 provides the averaged nightly means of the above, together with the mean distances at which they occured from the trap, the associated standard deviations and standard errors.

For the nights of the 6th and 8th, conditions were very similar and the averaged mean speeds lie within 2cm/s of each other, although the standard deviations for all of the averaged mean speeds (6th to the 11th) are large. This is demonstrated by Figures 34a, 34c, 35a and 35c, which represent the mean-groundspeed frequency distributions for the 8th, 10th, 9th and 11th respectively. It was mentioned earlier, in connection with the radial density calculations, that the plots hinted at the presence of a number of overlapping populations or species. If a single species only were present, the mean-speed frequencies would follow an approximately normal distribution. These figures are however characterised by a positive skew, indicating that a number of species were in the range of the imaging system. The combination of the individual species speed distributions gives rise, effectively, to a log. normal speed distribution, since each normal distribution must start from speed zero. Although this skew can be eliminated by performing a log.-transformation on the data, this is of little practical use since the resulting plot, which is symmetrical, reduces the impact of the available information.

TABLE 7

Averaged Nightly Groundspeeds, Accelerations and Angular Velocities

Date (1982)	Mean Speed (cm/s)	Min. Speed (cm/s)	Radial Distance of Occurence (cm)	Max. Speed (cm/s)	Radial Distance of Occurence (cm)	Max. Acce. (m/s^2)	Radial Distance of Occurence (cm)	Max. Decel. (m/s^2)	Radial Distance of Occurence (cm)	Max. Angular Velocity (Rad/s)	Radial Distance of Occurence (cm)	n
6/9	200	95.9	91.1	320	95.3	11.3	85.9	11.2	86.7	11.3	86.6	104
8/9	198	101	92.9	318	93.4	11.3	88.6	10.4	89.1	12.5	86.3	104
9/9	263	151	137	415	130	13.5	123	13.2	140	11.9	123	90
10/9	214	91.7	130	372	139	13.8	127	11.9	137	14.6	127	71
11/9	253	124	132	413	136	15.1	124	13.5	130	10.6	125	50
Standard Deviations												
6/9	65.7	74.6	36.3	98.6	43.1	6.42	38.0	7.48	32.8	6.99	36.6	
8/9	80.4	90.4	41.7	99.5	38.5	5.86	39.0	5.60	35.3	7.83	36.6	
9/9	111	122	57.5	127	53.2	6.18	50.4	5.91	52.9	8.93	49.9	
10/9	85.3	88.2	54.8	128	55.4	7.42	55.7	6.77	58.1	9.39	56.8	
11/9	94.8	96.7	53.2	120	51.2	7.50	45.9	7.00	46.7	8.68	50.9	
Standard Errors												
6/9	6.44	7.31	3.56	9.67	4.23	0.63	3.72	0.73	3.22	0.69	3.59	
8/9	7.89	8.86	4.09	9.76	3.77	0.58	3.83	0.55	3.46	0.77	3.59	
9/9	11.9	12.9	6.06	13.4	5.61	0.65	5.31	0.62	5.57	0.94	5.26	
10/9	10.1	10.5	6.51	15.2	6.57	0.88	6.62	0.80	6.90	1.11	6.75	
11/9	13.4	13.7	7.52	17.0	7.25	1.06	6.49	0.99	6.61	1.23	7.20	

This skewed speed distribution is not limited to the averaged mean groundspeeds, but is also true for the equivalent airspeeds (Figures 34b, 34d, 35b and 35d). It is important to note that the effect of increasing windspeed serves to compress the range of groundspeeds, when considering linear moth flight which is not subject to any form of illumination.

To investigate more closely the manner in which flight patterns changed at varying distance from the light source, the calculated minimum and maximum groundspeeds for each moth were coupled with their respective distances of occurence. For the nights of the 6th and 8th, the mean distance at which most minimum speeds took place within the viewing area was 91 and 93cm, against 95.3 and 93.4cm for the maximum speeds (Table 7). For all but the 9th, the "mean-maximum-speed distances" were all slightly greater than the mean-minimum-speed distances. Unfortunately, the sample sizes were not sufficiently large to show these differences as statistically significant (Table 8), since the trend is barely noticeable. Thus the p values are all greater than 0.1. It is quite possible, nevertheless, that with a large enough sample, the differences between these values would become significant. This cannot be proven directly by the values given in Table 7 , but subsequent analysis of other factors will show that these parameters are linked, on an individual basis, to both the luminous energy flux and the behavioural state of the animal.

Earlier it was stated that observation of the taped tracks revealed that speeds tended to increase with decreasing distance from the source; because of the large variance associated with both speeds and distances, in addition to the probable presence of a range of species, the relationship is not consistent but subject to considerable scatter. This can be seen from Figure 36a, a scattergram of maximum speed (linear) against distance of occurence for a sample of 104 moths taken from the 6th. In this case the slope is:

TABLE 8

Significance Tests for Mean-Minimum-Speed Distance v. Mean-Maximum-Speed Distance, and Mean-Maximum-Acceleration Distance v. Mean-Maximum-Deceleration Distance (Ground-Vectors)

Date (1982)	n	Mean-Min-Speed Distance v Mean-Max-Speed Distance	Mean-Max-Acceleration Distance v Mean-Max-Deceleration Distance
6/9	105	$p>0.1$	$p>0.1$
8/9	104	$p>0.1$	$p>0.1$
9/9	90	$p>0.1$	$p<0.05$
10/9	71	$p>0.1$	$p>0.1$
11/9	50	$p>0.1$	$p>0.1$

TABLE 9

Maximum Acceleration* v. Maximum Absolute Deceleration*

Date (1982)	a	b	r	p	n
6/9	6.06	0.47	0.55	<0.05	105
8/9	7.75	0.34	0.32	<0.05	104
9/9	7.34	0.47	0.45	<0.05	90
10/9	7.77	0.51	0.46	<0.05	71
11/9	10.01	0.37	0.35	<0.05	50

*m/s^2

TABLE 10

Maximum Angular Velocity[2] v. Mean Ground Speed[1], all tracks

Date (1982)	a	b	|r|	p	n
6/9	19.2	-0.04	0.38	<0.05	105
8/9	20.3	-0.04	0.41	<0.05	104
9/9	25.6	-0.05	0.65	<0.05	90
10/9	25.9	-0.05	0.48	<0.05	71
11/9	18.0	-0.03	0.32	<0.05	50

1) cm/s

2) Rad/s

$$v = 371-0.54 \times (r_t), \qquad (2)$$

where v is speed in cm/s, and r_t is distance from lamp in cm.

In support of this moderate trend ($r = 0.24$ and $p<0.02$), which does not resolve itself as significant in the smaller samples, the mean distances at which maximum accelerations take place are slightly smaller than for all the corresponding distances for the mean maximum decelerations (Table 7), although as Table 8 indicates these are mostly with a $p>0.1$. Both maximum acceleration and deceleration are however negatively correlated with distance (Figures 36b and 36c, with a $p<0.1$ and $p<0.05$. This apparent contradiction of maximum acceleration and deceleration occuring together is resolved when the two parameters are thought of as reflecting a generalised state of agitation and disorientation, which is inversely related to both the distance and intensity of illumination.

These three figures are extremely important, for they support, in a quantitative manner, the data presented by the TSMs. These highlighted density depressions, extending to 40cm around the light source, due either to a reduction in the numbers of moths entering this area or to increased speeds within it. Figures 36a and 36b show that maximum groundspeeds took place inside a radius of 20cm (the mid-point of the depression), as well as the highest accelerations. Although both maximum acceleration and deceleration are negatively correlated with distance from the lamp, no deceleration occurs within a radius of 30cm (Figure 36c). Bearing in mind the constant danger of anthropomorphism when interpreting insect behaviour, it still appears that this zone represents an area unfavourable to the flying moths.

Since acceleration and deceleration are both inversely proportional to distance from the light source the magnitudes of these two parameters are positively correlated. Table 9 provides the constant, a, the slope coefficient, b, the correlation coefficient, r, and the significance levels (deceleration is the independent variable), obtained for each night. The coupling of these parameters again suggests a state of disorientation, since any moth undergoing a rapid increase in speed is likely to similarly display a sudden decrease within the viewing area (see Figure 37). The magnitudes of these accelerations, typically $12m/s^2$ (i.e. 1.22g) may seem inordinately high when compared to accelerations common to the larger mammals (generally of the order of fractions of a g), but for such small animals they are not unusual. For example, Brown et al. (1968), when working in East Africa on Spodoptera exempta took long exposure (1s) photographs of moths flying close to a light-trap, and using multiflash techniques of 100 per second, observed moths performing complete rotations of 0.1m radius within 0.5 seconds, exerting a force of $15.8m/s^2$ (although this method provided a "framing" rate of 100Hz, it could not be used to provide a continuous record of events over 1 hour due to the obvious restrictions in the amount of data a single photograph can hold before it becomes unreadable). As a corollary to this, it would be expected that the greater the degree of turning and spiralling in a particular track, the lower the overall mean speed. The evidence for this is provided in Table 10 , where maximum angular velocity is correlated against mean speed, for each moth track. Not surprisingly, the magnitude of the rate of turning is limited by the forward speed of the insect.

Up to this point no attempt has been made to explain the form that the data has taken, nor to relate it to the changes which the Lepidopteran neurophysiology experiences when exposed to this kind of illumination. Moreover, no analysis has been made of

the catch; this is because none is possible. Astonishing as it may seem, from the estimated 1600 tracks seen within the viewing area over the five nights, a total of only 12 moths were caught, all but one of which were Noctuids (see Appendix D). This may seem improbably low (0.3% of the total number observed), but the next chapter will show in greater detail why this occured. A combination of factors were involved, including trap height, time of year and the location. The work done in 1983 was an outcome of the hypothesis developed in 1982 - that light-traps are extremely inefficient devices. Moths were virtually never seen to plunge directly into the baffles, but always underwent radical behavioural changes as emphasised in the preceding analysis.

After observing the tape recorded data, a further provision was written into the programme FLITRAP which analysed the following for each moth: when the minimum and maximum speed, maximum acceleration and deceleration, and maximum angular velocity occured, was the moth a) flying towards, b) flying away from or c) maintaining a constant distance from the trap? The manner in which this was calculated involved an examination of the data points immediately before (n-1) and after (n+1) the point in question; if the previous data point was at a greater distance from the trap then the one under study, and the one after it was closer, then the approach was positive. If the opposite was the case, then the approach was negative (i.e. the moth was receding from the trap). If (n-1) and (n+1) were both either closer or further away from the trap than n, the moth at that point was deemed as maintaining a constant distance, or "null" approach.

Table 11 contains the results of that analysis. For all nights, minimum speeds were associated with a positive approach at twice the frequency of those associated with a negative approach (for the 6th for instance, the

TABLE 11

Approach attitude Characteristics

a) Minimum Groundspeed v. Approach.

Date (1982)	Positive	Negative	Null	+ve/-ve Significance	n
6/9	55	21	29	$p<0.001$	105
8/9	45	24	35	$p<0.001$	104
9/9	45	19	26	$p<0.002$	90
10/9	30	11	30	$p<0.01$	71
11/9	33	10	18	$p<0.05$	50

b) Minimum Groundspeed v. Maximum Groundspeed, Null Approaches Only.

Date (1982)	Minimum Speed nulls	Maximum Speed nulls	p
6/9	29	11	<0.001
8/9	35	14	<0.001
9/9	26	7	<0.001
10/9	30	8	<0.001
11/9	18	1	<0.001

Significance between the positive and negative approaches - 55:21 - is $p<0.001$). The remaining approaches associated with accelerations are not of as much interest, but the association between minimum speed and approach attitude, together with the time surface matrices, is sufficient to show that the conventional idea of photo-tropotaxis when applied to nocturnally active Lepidoptera is at the least defective and at the most quite wrong. It is not surprising that more minimum speeds occur when moths are maintaining a constant distance from the trap than for the maximum speeds ($p<.001$ for all cases), since a "null" approach would happen at the point of turning from the trap, necessitating a reduction of groundspeed.

3.5. The Influence of Windspeed upon Dynamic Flight Strategy

Referring to the sample output of the programme FLITRAP given in Figure 12, calculations were performed by the programme which produced a second set of speed and acceleration values once the wind components had been vectorally subtracted from the measured groundspeeds. This was performed only for the track data taken from the 8th to 11th September, because the DVA probes were not operational on the 6th, and the Porton anemometer does not have sufficient temporal resolution to enable this kind of detailed calculation.

Mention has already been made of the possible danger in merely subtracting the wind components and assuming the remaining parameters are those which the moth had "intended". It is possible nevertheless to produce from this processing both interesting and accurate accounts of the dynamic situation. To elucidate, a single species of moth may be observed to have certain speed characteristics during flight around a light-trap under completely calm conditions; in windy conditions these characteristics will inevitably change but if, having subtracted the wind vectors, the resultant parameters are

still different from those in calm air, then it may be safely assumed that the moth is modifying its behaviour to suit the different meteorological conditions, and as a consequence incorporating these into its dynamic flight strategy. Although there were no completely calm nights from the 8th to 11th, wind conditions varied considerably and the calculated moth airspeed values were not identical from night to night. A further complicating aspect is the fact that the flight tracks are never linear, but usually comprise a series of sudden turns or revolutions around the trap. This becomes an important factor during the interpretation of the analysed data.

Both FLITRAP and the time surface plots have shown that a typical track will include flight with and flight against the wind, the latter taking place as the moth holds its position downwind from the trap. This may rarely take the form of hovering but in most cases it involves weaving about some arbitrary point. Under conditions of moderately strong windspeed, groundspeeds are positively correlated in a linear fashion to windspeeds. Table12 provides the statistics obtained from regressing mean groundspeeds of each individual moth against windspeed against that time, and the Figures 38a to 38d. show moth mean groundspeeds (dashed line) overlayed with windspeed (solid line). Windspeed is seen to exert a thresholding influence which is not evident below 1m/s; thus the correlation for the 8th is not significant ($p>0.1$). On the 9th, despite considerable scatter the measured groundspeeds can be seen to follow the windspeed ($p<0.02$), especially between track numbers 27-62, during which both windspeed and groundspeeds fell below their respective nightly means, although the windspeed was still above 1m/s. Figure 38d for the 11th displays this trend much more strikingly, but because of the scatter and the smaller sample ($n=50$), p only becomes significant (<0.1) if log. values are taken for both windspeeds and groundspeed. This scatter is attributable to two major causes:

TABLE 12

Mean Groundspeeds v. Windspeeds (cm/s)

Date (1982)	a	b	r	p	n
8/9	171	0.35	0.13	>0.1	104
9/9	130	0.82	0.24	<0.02	90
10/9	223	-0.05	-0.01	>0.1	71
11/9	191	0.26	0.18	>0.1	50

TABLE 13

Mean Airspeeds v. Mean Groundspeeds (cm/s)

Date (1982)	a	b	r	p	n
8/9	28.8	0.85	0.94	<0.001	104
9/9	74.4	0.71	0.76	<0.001	90
10/9	151	0.47	0.46	<0.001	71
11/9	154	0.34	0.30	<0.05	50

1) each individual moth will display a wide speed range due to the strong disorientation effect of the trap;
2) each species present will also possess its own typical speed range.

It is very likely that study of a single species of moth would reveal a closer relationship between windspeed and groundspeed.

Table 14 contains the averaged nightly mean airspeeds, together with the mean track lengths for these nights. The averaged nightly airspeeds do not differ significiantly from the equivalent groundspeeds given in Table 7, which suggests that during the time that the moths were in the view area, flight both with and against the wind took place. In light winds, the airspeed values are closely related to the groundspeeds (see Table 13), but as the wind rises in strength these two parameters become increasingly decoupled. This is well illustrated by Figures 39a-39d. Furthermore, although there is no significant difference between the averaged nightly groundspeeds for the 8th and 10th, ($p>0.1$), there is a highly significant difference between the airspeeds for the same nights. ($p<0.001$). Because the groundspeed frequency distributions are also similar (Figures 34a and 34c), which indicates a similar species range, the difference between the airspeeds is almost certainly due to the modification of dynamic flight stragegy to suit the altered meteorological conditions.

How then, can we account for the fact that both groundspeeds and airspeeds increase in direct proportion to the windspeed? In moderate to high windspeeds, airborne moths which have no selective migration strategy would tend to fly with the wind and the groundspeeds rise accordingly. The moths that entered the field of view usually entered from upwind, and at this stage the groundspeeds thought not necessarily the airspeeds would have been higher than those for moths in calm air. Once close to

TABLE 14

Mean Airspeeds and Track Lengths

Date (1982)	Mean Airspeed (cm/s)	Standard Deviation	Standard Error	Mean Track length (20ms)	Standard Deviation	Standard Error	n
8/9	196	72.1	7.07	62.9	36.7	3.60	104
9/9	262	105	11.1	68.7	41.5	4.37	90
10/9	253	87.2	10.4	65.6	42.3	5.02	71
11/9	241	110	15.6	56.2	33.3	4.71	50

the light source, behaviour is critically affected; in windspeeds which are well below the maximum airspeed of the observed moths, the mean track lengths did not vary significantly from night to night (Table 14), and since most time is spent downwind from the trap, in order for them to maintain their position, higher windspeeds demand an increased airspeed.

If the windspeed is greater than a moth's maximum airspeed, it is not possible for it to hold a static position relative to the trap. The limiting influence that wind exerts on moth behaviour implies that light-traps suffer from more than the disadvantage of being behaviouristic sampling devices; catch will be reduced on nights of high wind not only because certain species might become airborne in lower numbers with increasing wind, but also because in strong winds a small insect will find difficulty in manoeuvring around an object stationary with respect to the ground. The ratio of importance of these two wind factors cannot be decided by either the 1981 or the 1982 work, but some attempt was made in 1983 to answer this (Chapter 5).

The presentation of the density distributions around the light source with regard to the influence of wind has so far been largely descriptive of the results produced by the time surface matrices. To examine this influence on a quantitative basis, a final set of scanning programmes was written which produced angular density histograms for the moth tracks, i.e. how much time was spent in each of sixty sectors about the trap, of 6^{o} spread. To complement these, linear wind-rose diagrams were also produced for the 8th to 11th September.

Standard techniques are available (Mardia, 1972) which enable the calculation of circular angular mean and standard deviation ($\bar{x}o$ and so respectively). Table 15 gives the values for the angular density distributions of the track data from the 6th to 11th, together with the same

TABLE 15

Circular Statistics - Moth and Air Movement Distributions

Date (1982)	Moth Distribution			Wind Distribution			
	$\bar{x}_o$ (deg)	s_o (deg)	n	$\bar{x}_o$ (deg)	s_o (deg)	n	(Speed m/s)*
6/9	5.49	77.9	6655	186	-	-	0.89
8/9	66.7	79.0	6537	220	36.9	36000	0.84
9/9	56.1	74.2	6181	220	9.45	36000	1.70
10/9	78.8	54.1	4661	236	12.3	36000	2.01
11/9	273	68.5	2810	115	15.1	36000	2.66

*Windspeed values corrected to trap height.

statistics for the wind data. The circular distributions for both track and wind data are contained in Figures 40 through to 42 .

Clearly the angular density is strongly anti-correlated with the mean wind direction. This anti-correlation ranges from $176^{o}(\bar{x}o_{w} - \bar{x}o_{m})$ on the 6th, to 153^{o} on the 8th. Taking the mean position is not sufficient to account for the influence of the wind however, as it says nothing of the spread of the data. Now this spread will be controlled by five major factors:

1) the asymmetry of the light-trap;
2) the predominant migration orientation;
3) competitive illumination;
4) the strength of the wind;
5) the variability of the wind.

Factor (1) may be safely ignored since the trap was as radially symmetrical as possible. The importance of factor (2) cannot be assessed with certainty, although a number of moth species have been observed to migrate southwards in the winter months (Baker, pers. comm.), In addition, competitive illumination (the third factor), as can be seen on the fieldwork map (Figure 2), which shows a housing estate south east of the experimental location. Of greatest importance was the presence of a street light, positioned about 110m from the trap. Owing to the distance, it is unlikely to have had a great influence but there is some evidence to suggest that the radial distributions were affected. On the nights of the 8th, 9th and 10th, the perfect anti-correlation with the mean wind direction would have been 40^{o}, 40^{o} and 56^{o} from North respectively, yet all $\bar{x}O$ values display a slight Easterly bias, i.e. 67^{o}, 56^{o} and 78^{o}. Similarly, the radial distribution of the 11th is displaced from a perfect anti-correlation with the mean wind direction, from

295° to 273°, i.e. towards the south. If these radial distributions were indeed displaced by the street lighting, or by a general migration heading, then it is also possible that the entrance angle for many moths would not lie exactly with the wind flow; without further analysis it is not possible to demonstrate this conclusively, but the minor peak in the angular density distribution (Figure 42b) between 111° and 135°, which represents entrance angle, is biased towards the south (relative to the prevailing wind direction), by approximately 10°. Whilst factors (4) and (5) would influence the variance, only a relatively constant condition such as (1), (2) or (3), would account for the above bias.

Factors (4) and (5) are inter-related in determining the variance. Not only is this variance inversely proportional to wind strength, but it will be equally determined by its variability. On the night of the 10th, the mean windspeed was 2.01m/s with a circular standard deviation of 12.28°, and a circular standard deviation for the angular density distribution of 54.1°. On the 11th, the mean windspeed was considerably stronger (2.66m/s) yet the standard deviation of the density was higher - 68.53°, since the wind direction standard deviation was also greater, at 15°.

3.6. 1982 Analysis Summary

The outstanding features which emerge from the study of the above data may be summarised as follows:

1) The change in the flight pattern of an airborne moth (behaviour) when suddenly exposed to a directional source of light is radically different to the change brought about by gradual exposure to an omnidirectional source, given similar emission frequencies; the first involves escape, the second a number of behavioural components resulting in disorientation.

2) Because of the disorientation, moth response to MV125W light-traps is not simply a phototactic one; this was shown initially by the TSMs which revealed that:

   a) density fell to a minimum immediately around the trap;
   b) angular density distribution was closely related to even light winds.

3) The radial density calculations gave quantitative support for (2a) above.

4) The analysis of the dynamic flight strategy showed that both positive and negative accelerations increased with decreasing distance from the trap, lending support to the disorientation hypothesis, and that minimum speeds were most likely to occur during flight towards the trap. In addition, a number of overlapping populations or species were shown to be present.

5) Under light to moderate windspeeds airborne moths modify their behaviour to suit the conditions, altering their airspeeds. In windspeeds above terminal airspeed, accurate interpretation is not possible and the operation of light-traps is critically affected.

6) The analysis of the track angular density distribution and the associated linear wind roses provided quantitative support for (2b) above.

CHAPTER FOUR

DISCUSSION AND INTERPRETION OF THE OVERHEAD MOTH-MONITORING STUDIES

4.1. Introduction

The phenomenon of moth flight towards localised sources of light has been recorded throughout history, and yet all attempts to explain the reason for its occurence have been subject to limitations and exceptions. Most animal behaviour can be explained on an evolutionary basis, i.e., its adaptive significance to the survival of the individual or the species. The concept of adpative significance has proven to be an invaluable tool for behavioural ecologists, enabling many forms of behaviour to be linked to the relevant cultural or environmental stimulus which may otherwise have remained hidden. Adaptive significance is therefore a parsimonious theory, seeking explanations which are sufficient - and only sufficient - to account for a set of observations. In the following discussion the principles of adaptive significance will be adhered to but in a less common form - that of interpreting a set of actions which are not normally displayed by an organism.

4.2. Aspects of Phototaxis

An organism which displays a directed response to a light stimulus is said to be phototactic. With moths the response is mediated by both compound eyes (and to a much lesser extent by the dorsal ocelli), and stimulation of the one usually causes the moth to turn towards the source in order to equalise the effect on the other. Moths therefore respond to both the intensity and the directional component of the light and are properly termed photo-tropotactic. Because moths are considered to be attracted to light, they are usually more simply described as positively phototactic.

Unfortunately the statement that moths are merely positively phototactic is fraught with so many qualifications that is is virtually useless; firstly, very few tactic displays are enduring but are often extinguished after a certain time of exposure, depending upon the species and the physiological state of the animal. Secondly, many photo-tropotactic insects after having had one eye blinded, move in circles or spirals for a while when presented with a source of light, but at some point switch to photo-telotaxis, that is they learn to compensate and again move directly towards the light. Lastly, it is not enough to label an organism as phototactic without providing an explanation as to why it should be so on an evolutionary basis.

It is a well known fact by all entomologists working with night flying Lepidoptera that the most effective wavelengths for their capture are in the ultraviolet, between 340 and 400nm. What is less well known - and quite startling - is that electro-physiological experiments performed by Mikkola (1972) have revealed that the Lepidopteran retina is only 20% as sensitive to UV as it is to the yellow/green bandwidth (490-550nm), yet the capture ratio for these frequencies was 7.7:1 in favour of the UV. Moreover Mikkola showed that a combination of these frequencies using an MV lamp resulted in a doubling of the UV catch rate. It is important to note that in all these experiments the output energies for the different frequencies were all approximately the same.

4.3. Lunar Influences

Many insects respond in a similar fashion when exposed to a large variety of light sources, both with respect to spectral composition and intensity. Most hypotheses attempting to explain these effects have endeavoured to relate them to environmental factors commonly experienced by the various orders, that is, to sources of natural illumination.

The influence of the moon on trap catch and Lepidopteran activity generally has been studied more than any other single factor and is still the least well understood. Williams (1936) originally thought that trap catch was depressed during full moon due to a competitive effect, but after experimenting with light and suction traps simultaneously (Williams and Singh, 1956), he revised his opinions and considered that the higher ambient illumination reduced overall activity or possibly induced the moths to fly at a greater altitude. Nemec (1971) supports the idea of reduced activity after reporting that oviposition was depressed at full moon for Heliothis zea. Bowden (1973) suggested that Nemec was slightly in error concerning his observations, maintaining that peak oviposition occured just after full moon and that a marked assymetry in activity existed between the first and third quarters. This assymetry has also been found by Vaishapayan and Shrivastava (1977), who again caught the lowest numbers during full moon, but always caught more in the ascending quarter than in the descending quarter. A possible mechanism for this assymetry may be that Lepidoptera respond to the polarisation of moonlight (Nowinsky et al., 1979), using it as a migration cue. Theories which hold that moths are attracted to light because of confusion with the moon are based on the notion that they normally orientate by maintaining some angle relative to the moon, and if migration is not to follow a specific route then there is no compensation for azimuth during the course of the evening (Sotthibandu and Baker, 1979). In attempting to maintain a constant angle to an artificial source, which unlike the moon is not at an effectively infinite distance, the moth eventually spirals into the source and is caught.

In support of this theory, Sotthibandhu (1978) has demonstrated that the response distance of N. pronuba to a 125W MV lamp raised 9m above ground level is much greater than for the same lamp at only 0.6m. Whilst it is true that many species of moth caught by light-traps remain relatively

unaffected by moonphase, such as the cutworm moth (Hardwick, 1972), this does not necessarily imply that the airborne density - and therefore behaviour - remains similarly unaffected. If, as Sotthibandhu has shown, the response distance to a lamp changes as its angle of elevation changes (and also the angle of its diameter as perceived by the insect), it implies that moths have the ability to discriminate between real and "false" stimuli, and that this ability is a dynamic process, i.e. it is constantly being re-evaluated. Moths will rarely be unconditionally attracted to an artificial source merely because it is another bright object, and the greater the discrepancy between the source and the moon (with respect to position and emission spectrum), the greater the degree of disorientation evoked in the flight behaviour of a moth close to this source.

4.4. The Significance of the UV Bandwidths

Because of the particular effectiveness of the UV bandwidths in influencing moth behaviour, a numberof theories have in the past been suggested which identify naturally occuring sources of UV as ones to which moths may regularly be exposed. Certain species for instance display sexually dimorphic fluorescence with regard to wing patterning, and Fremlin and Nash (1983) propose that this may play a role in mating strategy. Disappointingly, experiments which used a UV source pulsing at the wingbeat frequency of the species concerned have actually resulted in a slight catch reduction. When both UV and pheromones were used in combination in order to mimmick a sexually receptive female, catches were reduced by up to 17.6% (Lam and Baumhover, 1982). In addition, such an hypothesis does not allow for the fact that catches from mercury vapour lamps are usually double those from UV traps, given the same output power (Walker and Galbreath, 1979, Labanowski, 1980). It would seem then, that the combination of the wavelengths from 350-400nm and 490-550nm has an effect greater than the sum of the individual components.

4.5. Towards an Integrated Approach

In 1960 Mazokhin-Porshnyakov proposed the idea that moths flew towards light sources rich in the ultra-violet because they mistakenly took these as indicating open sky, since much of terrestrial nature, especially green foliage, absorbs UV wavelengths; the open sky therefore remains as the only extensive source of UV radiation. Since this UV radiation originates originates predominantly from the moon, and to a lesser extent from the stars (Fremlin and North, 1983), the lunar theory of moth attraction to light is equally well accommodated within the framework of the Mazokhin-Porshnyakov hypothesis. The success of tungsten filament bulbs in attracting insects could also be accounted for by this hypothesis. Although their emission spectrum is shifted towards the longer wavelengths as compared to MV lamps, due to their operational temperature (Appendix A, Figure A4), the radiation reflected by the moon is altered not only with respect to intensity but also frequency composition, relative to the sun. Normalising to the emission at 555nm, the moon outputs half as much energy at 444nm than does the sun, and 1.06 times as much at 633nm, caused by the absorption characteristics of the surface dust (Henderson, 1970). Hence rather than appearing as a pure white disc, the moon has a somewhat yellowish quality.

A theory is only as good as its predictive ability, and if the above is at least partially correct then certain changes in moth flight behaviour should be expected under certain conditions. Specifically, when there is increased lunar illumination, light-trap catches should be depressed but numbers in the air should actually increase, and perhaps fly at a greater altitude. Because of the rarity of aerial sampling studies it is impossible to demonstrate this conclusively, although Brown and Taylor (1971) showed that the aerial density of nocturnal Lepidoptera in East Africa peaked at new and full moon. To counter this however, it must also be remembered that above a certain level of illumination nocturnal moths will not fly due to the increased danger of predation.

The attractiveness of a light source will not only depend on the intensity and emission spectrum, but also on the area of illumination. Many workers have found that the majority of moths affected by the light are not caught but sit in large numbers on the ground around the trap (Hartstack et al, 1967). Hollingworth (pers. comm.) discovered that a light-trap could be made much more effective by placing it against the white-washed wall of a building, onto which the moths would settle and remain motionless. Traps which incorporate white baffles and lamps often show an increase in catch rate of 400%. (Mizotani et al, 1982, Novak, 1983).

Further evidence which lends support to the Mazokhin-Porshnyakov hypothesis has been provided by Smith and Cantello (1971), who researched the efficiency of two types of UV trap. The first used four 15W BL tubes arranged at the vertices of a square (about 30cm along the diagonal), on top of a collecting cone. The second used the same collecting cone and four tubes, but these were arranged in a row to provide a "wall of light". The catch ratio for the tobacco hornworm moth was 1.14:1 in favour of the in-line trap, these results having been obtained after sampling for one hundred nights.

The above hypothesis is far more plausible an explanation of the manner in which light affects moth behaviour than any of the previous ideas discussed, but without further elaboration it still fails to reconcile a number of theoretical and observational difficulties. Without qualification, it still assumes that a moth is unconditionally attracted due to a misinterpretation of the stimulus. Likewise, it cannot account for moths which escape or remain unaffected, nor can it explain the extreme changes in the flight pattern of individual moths close to a light. Despite these objections, in the following section it will be shown that the Mazokhin-Porshnyakov hypothesis is not defective, but merely incomplete.

4.6. An Elaboration of the Mazokhin-Porshnyakov Hypothesis

We have already seen that moths, when presented with a stimulus to which there is no appropriate response in the behavioural repertoire, exhibit an unconditional escape reaction. What all of the above hypotheses ignore is that there is almost certainly two stages involved with changes in the flight pattern of a moth when flying towards a universally visible source. Firstly, there is what may be termed a long-distance attraction response, R_a, and secondly a short-distance escape response, R_e.

At a considerable distance from the trap the angle which the light subtends at the eye of the moth will change little as the moth moves, and the energy flux (depending upon the distance), will be low. Bowden (1975) considers that at 519m, the energy flux of the 500-600nm bandwidth emitted from a 125W MV bulb is equivalent to that reflected from the new moon. It is quite possible, as Mazokhin-Porshnyakov suggests, that at the early stages nocturnal Lepidoptera misinterpret artificial light sources as pointers to the open sky or moon, and react accordingly by flying towards them or by attempting to maintain some constant angle with respect to the image subtended at the eye.

As a moth nears the source, various other factors start to predominate which indicate that the light is not a natural source; the angle subtended at the eye changes substantially as the animal moves, the light is not diffuse but a point source, the elevation is wrong and most importantly, the energy flux is changing too quickly with distance (using these factors it may therefore be possible to estimate the effective range of a light source, if its physical characteristics are known). Superimposed on the attraction response, the escape response begins to operate which, like R_a, increases with decreasing distance from the trap. R_e differs from R_a however, in that it appears later but when it does it increases more rapidly.

The integrity of this hypothesis rests with its ability to predict behavioural change (although this cannot prove it), and it can now be checked against the results obtained from the 1982 analysis. In particular, these behavioural changes should arise not from the influence of either R_a or R_e separately, but since they occur simultaneously, from their summation. R_e is essentially antagonistic with respect to R_a and the summation is therefore $R_a - R_e$. As a moth nears the source under the predominant influence initially of R_a, there should be little to indicate any disorientation in the flight path. Thereafter as R_e increases, it should be expected that within a certain distance from the light, the moth begins to reduce its speed of approach, i.e. minimum speeds should be recorded during the approach phase. Furthermore, since R_e increases more rapidly than R_a but starts later, at a certain radius from the trap the resultant of $R_a - R_e$ will reach a peak, representing the optimum distance of attraction. Movement either towards or away from the light causes a reduction in the strength of the $R_a - R_e$ resultant, such that the moth will seek to maintain this optimum radius. Because of the instabilities induced by local wind vectors and the moth's own inertia, as well as the energy required for hovering flight, its movements will oscillate about this optimum radius. The rapid fluctuation of the responses will cause the moth to fly in an erratic manner quite a typical to its normal flight strategy.

All of these expected changes have been shown to take place for the moth tracks recorded around the 125W MV lamp mounted at 5.0m and 7.1m. The TSMs and the collapsed field plots of the radial density distributions place the maximum density around the lamp in light winds at around 40cm. The reduction in time spent at distances closer than this could be attributable to three causes:

1) moths enter this region as often as any other but are subsequently caught, and no time is therefore spent in flying away from the trap;

2) moths enter this region as often as any other but here fly at greater speeds, thereby reducing the time-density;

3) moths simply enter this region less frequently than any other.

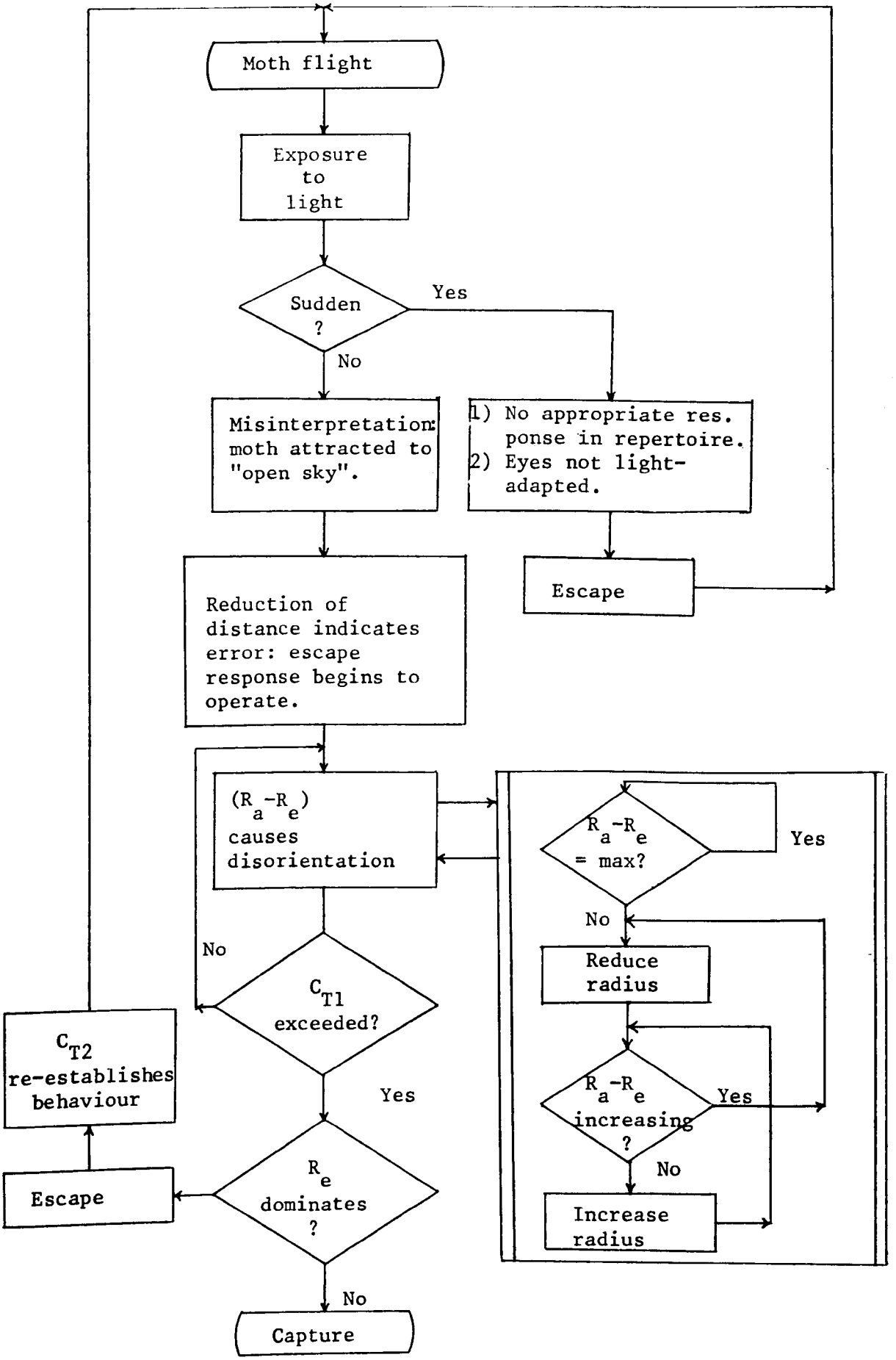
The first possibility can be discarded, since (as previously stated) the catch over the five nights was negligible. The reduction in density close to the trap is due to a combination of possibilities (2) and (3) above, since the assumed rapidly increasing response R_e at distances under 40cm would induce higher airspeeds involved with escape. Indeed, as Figure 36 shows, speeds tend to increase with decreasing distance from the trap, yet these are associated with negative approaches. Similarly, the minimum speeds, induced by the changing R_a-R_e value, are associated predominantly with positive approaches (Table 11).

So far the modified Mazokhin-Porshnyakov has been used to explain on a quanlitative level the type of pattern that emerges from the analysis of large numbers of moth tracks. With individual moths, certain time-constants operate which are irrelevant when considering a large sample. For example, a single moth which flies around a trap will eventually either fly off or more rarely, be caught. Thus the concept of the R_a-R_e resultant is time-dependent, and after this time is exceeded one response will dominate. If the moth escapes, then it may be influenced at a later stage by another light-trap. A second time-constant is also involved, one which determines the length of time necessary for the re-establishment of the extinguished response. It is not, unfortunately, a simple

matter to estimate the duration of these time constants. Not only will they almost certainly be species dependent, but it is highly probable that environmental clues will play a part in determining their length. For instance, moths which flutter around domestic light bulbs (inside a room) will often dip and weave for some minutes before alighting on a wall or ceiling, to remain motionless, in some cases, for hours. Hence both the first and second time constants, due to the complete absence of familiar stimuli, may be much longer than they would be under a night sky. The fieldwork suggested that under natural conditions, the first time constant was of the order of seconds and the second one may well have lasted for only a few minutes. The idea of opposing drives is a common one in behavioural biology, the one acting as a control to the operation of the other. When they occur together, as in this instance, a selective response extinction mechanism is necessary if the organism is not to become exhausted.

Unfortunately, all biological hypotheses or models have their limitations, and this is no exception. Drive theory is an acceptable form of behavioural analysis for invertebrates but is quite inappropriate for the higher mammals. This hypothesis was developed to explain large scale changes but it cannot predict what an individual moth will do - it can only describe why the density structure takes the form it does after repeated track-events. Whilst the R_a/R_e hypothesis is consistent with the collected data, it is ultimately an interpretation since it is impossible to analyse changes which occur at a neurphysiological level.

With these limitations in mind, the following paragraphs will develop the hypothesis on a more quantitative basis, relating it back to the distributions observed, and by the use of statistical tests, examine the validity of the theoretical distributions. The modified Mazokhin-Porshnyakov hypothesis is given in flow-chart form overleaf, and may be


Moth flight
Exposure to light
Sudden ?
Yes
No
Misinterpretation: moth attracted to "open sky".
1) No appropriate response in repertoire.
2) Eyes not light-adapted.
Escape
Reduction of distance indicates error: escape response begins to operate.
$(R_a - R_e)$ causes disorientation
$R_a - R_e$ = max?
Yes
No
Reduce radius
$R_a - R_e$ increasing ?
Yes
No
Increase radius
C_{T1} exceeded?
No
Yes
R_e dominates ?
Escape
C_{T2} re-establishes behaviour
No
Capture

briefly summarised in algorithmic form as follows:

1) Moth exposure to light:

   a) sudden - unconditional R_e due to
      i) unfamiliar stimulus,
      ii) eyes not light-adapted.

   b) Gradual - misinterpretation of stimulus leading to:
      i) approach - R_a increasing;
      ii) R_e beginning to operate due to environmental clues that the stimulus is unfamiliar.

   c) Resultant of R_a-R_e reaches a peak, leading to disorientation:
      i) approach and retreat;
      ii) sudden speed changes;
      iii) circling of light-trap.

   d) After time-constant No. 1, one response dominates, leading to escape or capture.

   e) 2nd time constant determines re-establishment of extinguished response.

   f) Return to (1).

4.7. Quantification of the R_a and R_e Components

Although both the R_a and R_e components increase with decreasing distance from the trap, one of the assumptions upon which this hypothesis is based is that they do not tend to infinity as r_t tends to zero, but to some finite value. This value will be determined by the physical nature of the lamp, itself subject to finite limitations. Thus each individual component may be thought of as following a one-

sided Gaussian distribution, normalised to unity, i.e.

i) attraction $\alpha\ e^{-(r^2/a)}$ (1)

ii) escape $\alpha\ e^{-(r^2/b)}$ (2)

The combination of these components should result in a curve which describes the radial density distribution shown by the collapsed-field plot of Figure 43d, for the 6th and 8th September combined. At this point we are still attempting to establish the theoretical distribution for a large number of moths in calm conditions, flying around a 125W MV bulb, ignoring the minor disturbances of captured and escaped individuals. Why then, are we using as a basis for this distribution the plot of Figure 43d which was taken from two evenings during which there was an air movement of about 0.8m/s? There are two reasons for this: the first is that absolutely calm conditions very rarely happen, and these were the calmest evenings available. The second is much more important - in Chapter 3 it was demonstrated that whilst light winds influenced the density distribution in the area around the trap, they would not shift the distance at which the density peaked (radial densities) as they were well under the maximum airspeed capability of the moths. The reason why light winds influenced the area distribution is because moths cannot fly backwards relative to the air movement, and this would have been necessary if the moths were to maintain a constant position upwind from the trap (the upwind density is never zero however since moths did not hover but usually weaved about a certain radius).

Figures 43a through to 43c show how the individual components are combined in order to produce the theoretical radial density curve of Figure 43c, in which the lamp would be situated on the x-axis. Note that the density here is not zero, as this would imply a zero catch rate, which is obviously incorrect.

Figure 43d shows this curve overlayed on the radial distribution for the 6th and 8th combined, normalised to a suitable scale. The correlation coefficient is here R=0.96 with p<0.001.

In calm conditions therefore, the radial distribution takes the following form:

$$d_r = \{e^{-(r^2/a)} - e^{-(r^2/b)}\}. k \qquad (3)$$

where a = 500 and

b = 25 and

k is some normalising constant, the value of which will be determined by the total number of track events.

The three-dimensional representation of this distribution can be produced by rotating the above equation about the y-axis as shown by Figure 44 , for absolutely calm conditions. Since b is smaller than a, R_e starts later (when considering flight towards the lamp) but rises much more sharply than R_a. Note that as r->0, both R_a and R_e ->1.

Figures 45aand 45b show how the radial density distribution changes when conditions progress from still air to light winds; again it must be stressed that only the amplitude changes and not the form of the distribution. The radial density upwind is flattened and the downwind density emphasised, the magnitude of each being determined by the strength of the wind. To reproduce the three-dimensional image which would give the area density, the amplitude of the curve must be related to the angle it subtends to the flow of the wind. Examination of the angular density distribution plots shows that in practice, for light winds, this follows a cosine response (see especially Figure 40). The plot of Figure 46 represents an ideal area density distribution occuring around a light source with the wind blowing from the south at 0.8m/s.

In light wind conditions below the maximum airspeed capability of most Lepidoptera, the ratio of the downwind: upwind peaks is 3:1, and changes gradually as the angle changes relative to the wind, hence:

$$d_r = (1 + w \text{ Cos } \theta).\{e^{-(r^2/a)} - e^{-(r^2/b)}\}. \quad k \qquad (4)$$

where w represents the influence that the wind exerts on the density distribution, and ranges from zero (in calm conditions), to unity.

This distribution can be checked against the distributions of the 6th and 8th, and gives regression coefficients of 0.8 and 0.7 respectively, and in both cases $p<0.001$. Since the ratio of the downwind:upwind peaks is 3:1, w takes the value 0.5. Hence the expression $(1+w\cos\theta)$ ranges from 0.5 to 1.5. The maximum amplitude differential with respect to the upwind and downwind peaks will take place when w=1, since the expression $(1+w\cos\theta)$ will range between zero and two; as the windspeed decreases w will also decrease, reducing this differential. This is a useful result, since the equation describing the distribution in calm air, given by (3) above, can now be replaced by (4) which is a general form of the equation, for windspeeds ranging from zero to 1m/s.

4.8. Additional Evidence in Support of the Elaborated Mazokhin-Porshnyakov Hypothesis

The fact that light-traps attract more moths than they catch is not a new one, for a number of researchers have attempted to quantify the way in which density changes with distance from the light source. Hartstack et al (1967) using trays filled with oil and water placed in concentric circles around a BL trap found that most moths were caught at a distance of just under 1m from the lamp, and that the area density was affected by the wind in a similar manner to that

described in this thesis. Hsiao (1973) attached cardboard baffles, painted matt black and coated with a sticky layer of adhesive, to a vertically mounted 15W BL tube. The moths caught were identified and radial density distributions were produced for each species. These distributions were remarkably similar to the distribution of Figure 43d, but with the optimum radii different for different species (see Figures 47a-47c). The cabbage looper for instance peaked at 45cm, whereas the beat armyworm peaked at around 23cm. Hsiao states:

> "the results reveal that the number of trapped insects first increases with distance from the lamp, reaches a maximum, and then decreases. The shape of the distribution and the distance of the maximum appear to vary with species of moths".

The identification of different peaks is significant as it confirms the same proposition given in Chapter Three. As to the reason for this differential attraction, this is a question which is almost certainly linked to the way in which each species has adapted to its environmental niche.

4.9. Limitations of the Elaborated Mazokhin-Porshnyakov Hypothsis

Equation (4) has only been tested against actual data for windspeeds below the critical threshold described in the preceding discussion. In reality, although strong winds (above 4m/s) would reduce the upwind density almost to zero, i.e. w->1 as the windspeed increases, well before this happened the very form of the equation would alter with regard to the coefficients a and b. This would happen to such a degree that it would no longer be of use as a predictive tool. The equation only holds for windspeeds which do not radically alter the position of the upwind and downwind peaks relative to the trap. As the radial densities of Figure 33a

through to 33d show, high windspeeds change the form of the distribution and not just the amplitude of the peak, well before reducing the upwind density to zero. Thus a and b must change, like w, at a certain point, but because they represent the behavioural components R_a and R_e and not environmental influences (unlike w), the validity of altering them is questionable (it is possible nevertheless that both the attraction and the escape responses are modified intrinsically by increasing wind, but it cannot be demonstrated).

A further criticism is that the equation is too general. The behavioural components change for different species, and they also change for a single species at different times. Labanowski (1980) recorded that the catch ratio between MV and BL traps for any one species was generally 2.5:1, but this ratio changed over the course of the evening. The change in these components could be due to changing internal factors but they may also be dependent upon external conditions such as temperature and the number of moths already caught. The equation (4) provies an adequate description of the data collected in Cranfield during 1982, but whether it would remain valid in Kenya for instance, where catch per hour of a single pestiferous species may be greater than a whole week's catch in Britain, remains to be seen.

Despite these reservations associated with the temporal and spatial variance of the coefficients, the general notion that light-traps operate by a disorientation process is more plausible than any other hypothesis to date. In all research where the behaviour of flying insects has been studied, the capture is never a straightforward operation. The underlying theory to the equation is based upon observations of British nocturnal Lepidoptera, but it is almost certain that the capture mechanism of light-traps is invariant even for different orders of insect.

One more conclusion can be drawn from the way in which the R_a and R_e component vary with distance. If they behave as Figures 43a and 43b suggest, then the density found in the immediate area of a trap may fall off very rapidly with distance (i.e. 1% of the maximum at 4m), but the actual distance of attraction (for a 125W MV lamp), depending upon the level of the ambient illumination, could be perhaps 100m. The area which could be viewed by the imaging system was not sufficient to provide an answer to this question, but the calibration work of the next chapter presents additional evidence that light-traps, whilst their radius of influence maybe as stated, have only a limited sampling efficiency.

CHAPTER FIVE

A CALIBRATION OF LIGHT-TRAP EFFECTIVENESS BY THE USE OF REMOTE SENSING (1983 Fieldwork)

5.1. Introduction

It is almost invariably the case in any field of research that along with each new discovery, there follows in its train a host of unsolved problems. With particular reference to the work so far discussed, some old problems which habitually interest workers in this area re-emerged once again, together with an entirely new set arising from the analysis of the 1982 data. It was fortuitous, then, that the combination of these two categories could be studied and some answers attempted (in part) by one single further field season. It must be stressed from the outset, however, that the nature of the work done in 1983 was certainly not a complete study, and most of the conclusions reached are no more than tentative suggestions.

Specifically, these problems for which some answers were sought in 1983 were as follows:

a) The effect of meteorological factors upon light-trap catch (1981) was to some extent quantified, yet the mechanisms were not understood - do certain species, for instance, become airborne in lower numbers with increasing windspeed, or does the air movement simply make it more difficult for them to manoeuvre into the trap? Either possibility would produce the same result, and the monitoring work of 1982 did not sample a sufficiently large volume of airspace to answer this conclusively.

b) A major point of concern was the large discrepancy in catch numbers between the two years; if, despite the fact that the weather conditions had been somewhat similar, the 1982 catch had been a fluctuation from the mean, then it would not be unthinkable to suggest that the whole of that year's behavioural results might be aberrant.

c) Most of the conclusions derived from the 1982 analysis relied upon the assumption that the flight patterns observed were caused by the proximity of a 125W MV light source, which far surpasses the intensity of any other form of illumination at that period under "natural" conditions. Although this was by no means an unreasonable assumption, to date no control had been set up in which moths were observed flying in a night sky with no more significant illumination than the stars and perhaps the moon.

Regarding problem (a), the solution here was clearly one of calibration, of which there are two parts:

i) comparison of numbers in a given volume of airspace per unit time against prevailing weather conditions;

ii) comparison of numbers in a given volume of airspace per unit time against a simultaneous catch in a 125W MV Robinson light-trap. This would result in an "effective trap radius", i.e. given a known density, the proposed radius would determine the numbers caught per unit time.

Problem (b) was by comparison more straightforward. In this case it was proposed to operate two light-traps, one at 1.4m and one at 7.1m, at approximately the same time of year and in the same locality as those which operated in

1981 and 1982. In this manner their catches could be compared to estimate whether or not the numbers caught in 1982 were indeed abnormal.

5.2. Choice of Monitoring Period and Location

The fieldwork of 1983 was once again carried out in the late summer, between 17th August and finishing on the 30th September. During this time, many nights were deemed unsuitable either because of prohibitively high winds (which commonly occur in the area at this time of year), or rain, both of which made the use of the electronic monitoring equipment unwise because of the possibility of equipment failure. As a result, out of a possible total of forty four nights' sampling, only ten provided suitable conditions for data gathering.

Figure 2 shows a map of the fieldwork site, with the two traps positioned along the grass strip used in 1981, with the one at 1.4m located furthest into the field. These were separated by 50m, a distance which was considered great enough for the traps to operate with minimal mutual interference. The camera and illuminator were positioned to the rear of the fieldwork hut, sampling a volume of space the mid-point of which was 122m distant from the 1.4m trap and 94m from the trap at 7.1m.

5.3. Illumination of the Aerial Sample Volume

The calibration was to be performed by illuminating a known volume of airspace with infra-red (780nm-2000nm) radiation, which, as far as is known, is undetectable by the Lepidopteran visual system. (As mentioned in the General Introduction, some controversy has arisen in recent years over the ability of moths to detect thermal IR. However, the very fact that so many experiments have been necesssary to

show that the ability for detection exists in this region, indicates that sensitivity here is very low).

A TV camera fitted with a 17mm focal length wide-angle lens and image intensifier operating in the continuous mode (and therefore the same as in the 1982 work) was focused on this volume and the images displayed on a monitor and simultaneously video-recorded. To shield the intensifier and camera from wind-buffeting as much as possible, these were placed in the fieldwork hut (before the Northward facing window), with the illuminator and its power supply in the field.

To enable an accurate assessment of aerial density, it was critical that the sample volume was precisely defined, so the illuminator chosen was that which was used in the 1982 directional beam experiments. In this case, however, an RG780 infra-red filter was attached to the front end. This is a low-pass filter which has a half-power transmittance point at 780nm, with a flat response from 850nm onwards. Figure 48 is a side-view diagram of the operational beam system. The illuminator, using a beam spread of 9^{o}, was positioned directly in front of the camera at a distance of 18.4m. As Shown, the beam was elevated upwards at an approximate angle of 10^{o}, with the camera elevated at 15^{o} (the precise values changed slightly from night to night. Refer to Table 16 for the actual values). The slight variations in the orientation of the equipment meant that for each night, the cross-sectional side-view area as seen on the monitor would vary by a correspondingly small amount. Calculation of this area was a relatively straightforward problem, and varied from between 10.5 and 15.19m^2. Estimating the volume was more difficult, for it involved the calculation of a volume for a non-regular solid - in effect the portion of a conical volume (the beam) contained within a more rapidly diverging pyramidal volume (the angle of view).

In order to calculate this volume, an integral was derived (K. Allsopp, pers. comm.), which could be used to calculate the volume enclosed by the shaded sector in the Figure below, giving

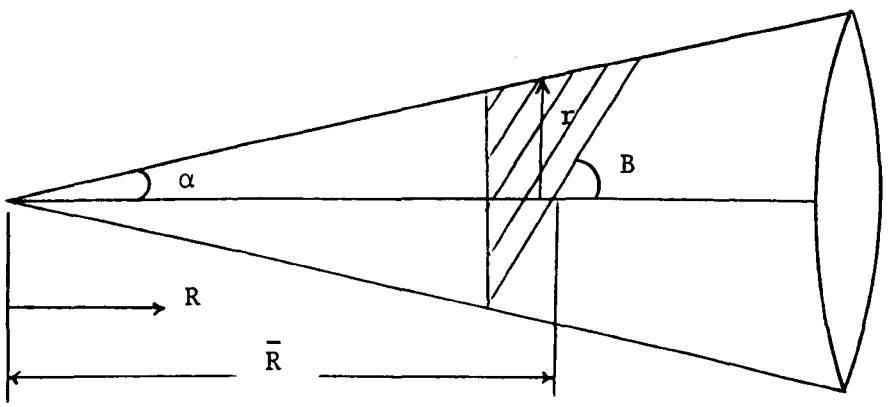
$$Vol = \frac{\bar{x}^{-3}}{\tan\alpha} \int_{-1}^{+1} \frac{\{(\pi - \cos^{-1} y(1 - y^2)^{\frac{1}{2}}\}}{(y + t)^4} \, dy, \qquad (1)$$

where $r = R \tan \alpha$

$\bar{x} = \bar{R} \tan \beta$

$y = (\bar{x}/r) - t$

$t = \tan\beta/\tan\alpha$



Referring once more to Figure 48 , this integral was applied to isolate the central sample volume. Using a standard numerical technique on a programmable calculator, the sample was found to be $25.7m^3$. This volume is in fact a mean of all the volumes found, but because of the errors associated with the density calculations (approximately 5%), it was not considered necessary to refine the solution to any further degree.

The method of forward-scattering, where light was reflected downwards and towards the camera by the wings of a moth, whilst still maintaining the same angle subtended to the horizontal, was the most efficient layout possible for using the available

lighting, and ensured good receiption for even small objects in the beam. If a reliable estimate of the flux was to be found, then it was essential that the orientation of the source/camera was as far as possible, perpendicular to the general flow of the wind, so on each night the direction of the wind was measured and the equipment positioned accordingly.

5.4. Calibration of the Monitoring System

Once the illuminator was fitted with an infra-red filter, the emitted intensity of the energy was greatly reduced (see Appendix A) and so it was necessary to perform a test to examine whether or not the imaging system could detect the smallest moth it was likely to encounter in any part of the sampled volume.

Figure 48 depicts the test layout used. A small noctuid was fastened to a thin metal rod, in turn attached horizontally to a 5m pole, at a height of 2m. Two other moths (the first another small noctuid and the other a geometrid) were fastened in a similar manner at 3m and 4m. Apart from the moths, which retained their normal colouring, the whole assembly was painted a uniform matt black. This apparatus was then positioned in the sample volume and moved backwards and forwards and from left to right, whilst an observer examined the image on the monitor screen. From this test, it was ascertained that the imaging system could satisfactorily detect all types of moths passing in any orientation through the sample volume.

5.5. Meteorological Data Recording

For windspeed recording, there was no necessity in this case to have an accurate second-by-second account of air movement, since it was total numbers and not individual flight

patterns that were of interest. It was sufficient then to measure the wind for 2min every 10min for the duration of the monitoring period, using a hand-held Lowne vane anemometer. Temperatures and humidity were recorded by the thermohygrograph described in Chapter 1, and these three variables were enough, it was felt, to account for most of the variance with respect to local flight density.

5.6. Operation of the System and Data Gathering

The method of collecting data from the monitoring system was a simple process - a count was kept for each moth that entered the field of view, together with its time of appearance. Because the data was recorded, it was also possible to measure time spent in the sample area to an accuracy of 1/50th of a second, and in addition some degree of track orientation (though this was limited since there was only a single camera) and of direction of flight in relation to the prevailing wind.

Each nightly sample period lasted for 1h, and this usually commenced 1.25h after sunset, thus becoming progressively earlier as the nights grew longer. After this period, the contents from the two traps were emptied and identified.

5.7. Presentation of Results

Table 16 contains all the information relating to the setting up and alignment of the equipment, including the maximum and minimum heights of the sample volume. The data collected is presented in Table 17 - mean windspeeds measured every 10min over the duration of the sample period, mean temperatures and finally the biological data. The column headed "Observed moth numbers" refers to all the moths which were detected by the imaging system. As mentioned earlier, the viewed cross-sectional side-view area varied from night to

TABLE 16

1983 Calibration Study: Equipment Settings

No.	Date (1983)	Beam Elevation (Deg)	Camera Elevation (Deg)	Minimum Sample Height (m)	Maximum Sample Height (m)	Sample area (m^2)
1	19/8	11	15	1.88	4.53	15.2
2	20/8	9	15	1.82	4.16	15.0
3	21/8	8.5	17	1.89	4.12	14.2
4	22/8	9	19.5	2.03	4.29	12.2
5	24/8	9.5	16.5	1.95	4.25	13.1
6	26/8	10	15	1.85	4.35	15.2
7	27/8	10	21	2.22	4.54	10.5
8	29/8	9.5	16	1.93	4.29	14.1
9	30/8	9.5	21	2.14	4.43	10.9
10	31/8	10	16	1.96	4.39	14.2

NOTES:

1) Source/camera separation was 18.4m in all cases, excepting 24/8, for which it was 18.1m.

2) Source beam emission angle was 9^{o}.

3) Horizontal:vertical view angle ratio on the rectangular monitor screen was 37.7^{o}:30.5^{o}.

4) The mean sample volume was $25.7m^{3}$.

TABLE 17

1983 Calibration Study: Environmental and Biological Data taken during Sample Period

No.	Date (1983)	Mean Windspeed (m/s)	Mean Temperature (^{0}C)	Observed Moth Numbers	Moth Flux (/100m^2/h)	No. Video Fields with data	Density, Method 1 (No/10^{6}m^3)	Density, Method 2 (No/10^{6}m^3)	Density, Method 3 (No/10^{6}m^3)	Catch at 1.4m	Catch at 7.1m
1	19/8	2.67	19.3	36	238	-	388	-	151	3	0
2	20/8	1.53	18.2	61	408	-	667	-	351	2	0
3	21/8	0.46	16.6	63	443	-	724	-	570	11	2
4	22/8	0	18.7	79	648	4199	1058	907.7	1058	26	8
5	24/8	4.1	15.6	7	54	-	87	-	26	0	0
6	26/8	1.03	16.5	46	303	-	495	-	308	8	0
7	27/8	1.56	17.4	42	402	-	657	-	342	4	0
8	29/8	3.07	11.5	14	100	-	163	-	58	1	0
9	30/8	1.52	14.9	35	322	-	526	-	278	8	-
10	31/8	0.94	20.7	67	472	3761	771	813	496	15	-

Note: Dash indicates figures not available

night, and so the column headed "Moth flux per $100m^2/h$ is the data recorded in the previous column normalised to a suitable scale. The last two columns are of total numbers caught in the MV traps mounted at 1.4m and 7.1m.

5.8. Preliminary Discussion

The moths caught in both the 1.4m and 7.1m traps during the sample period were all identified as belonging to the family Noctuidae, apart from 7 other individuals (a complete list appears in Appendix D). As the work was performed towards late summer in an exposed location, the numbers caught are low. With particular reference to the 7.1m trap, no moths at all were caught except on the 21st and 22nd August, when the windspeed measured at 2m was less than 0.5m/s. In the introduction to this chapter, it was stated in paragraph (b) that the catch figures of the 7.1m trap during the 1982 work were worrisome since they were so low. Similar numbers were caught in the same trap in 1983, which allayed any fears that the figures were atypical. Indeed, after the 29th August when for four days the trap had caught nothing, a decision was made to discontinue its use - in any case, no valid statistics could have been derived from this data.

As for the moths observed on the monitor screen, it was important that the infra-red beam had as small an effect as possible on their flight behaviour, if a reliable estimate of density were to be made. For all nights other than the 22nd August, there was air movement to a lesser or greater degree and on these nights, because the camera orientation was perpendicular to the wind direction, the vast majority of moths appeared to be flying with the wind and therefore across the monitor screen. On the 22nd, when there was virtually no air movement, moths entered the field of view from a variety of directions, but these were usually along the horizontal plane (any moths that did appear to be moving along the vertical

light equally well have been flying horizontally towards or away from the camera in the same axis; see Figure 48). There were certainly no major deviations or sudden movements in the flight patterns as were seen in the work of 1982; if the infra-red beam was visible, then the sensitivity in this region was so low as not to significantly interfere with any "normal" behaviour.

5.9. Forms of Analysis

The analysis of the biological data for 1983 can be summarised as follows:

1) the correlation of weather variables with the catch in the 1.4m MV trap;

2) estimation of flux (numbers per unit area per time) and density (numbers per unit volume) and the manner in which they change with weather variables;

3) the correlation of density with the 1.4m MV trap catch;

4) an estimate of trap effectiveness indicated by (1) and (2) above.

In Chapter One it was shown that regression analysis was valid as a statistical test for the data collected since, over the sample period, for any fixed value of the independent variable x (such as temperature) the corresponding value of y - moth numbers of a certain species that could turn up in repeated samples - followed a noraml distribution; in addition, the variance did not alter significantly with each of these distributions. With the 1983 data, however, a problem arises since it was not possible to identify to the species level any moths seen on the monitor screen (for this reason it is

not necessary or relevant to give here the species caught in the light-traps). What is known is that virtually all the moths caught belonged to the same family - the Noctuidae - and it is probably not too far from the truth to state that the vast majority of the moths that passed through the detection system were also noctuids. The season was chosen deliberately to ensure that most of the Noctuids caught would be at roughly the mid-point of their flight period, and so regression analysis would be a suitable tool for estimating the effects of weather factors, unbiased by a changing background population. Unfortunately, because it was not possible to identify individual species, the analysis was not centred around the derivation of individual slope coefficients as in 1981, but was limited to standard regression techniques (either linear or ln of y).

All things considered, this test was the most applicable for the investigation of weather influences on the aerial density of Noctuids, regardless of species, and of Noctuid numbers caught in the trap. Because of the limitations of the system used, it was not possible to correct for these imprecisions and any analysis must be similarly limited. Despite this, some effort has been taken to ensure that the results from the statistical examination are as accurate as can be realised.

5.10. 1.4m Light-Trap Catch in Relation to Meteorological Factors

The predominant weather factors affecting catch have already been shown to be temperature and air movement and of these, air movement becomes more critical when the air temperature lies above the flight threshold of the Lepidoptera for a given location. This can be readily shown with the 1983 trap catch data by performing single variable regression for temperature as follows:

$$\ln(\text{catch}) = -1.46+0.191(t) \qquad (2)$$

with t in ^{o}C. In this case, the estimated correlation coefficient, r_{12}, is 0.492 and $p>0.1$.

For windspeed (in m/s),

$$\ln(\text{catch}) = 3.03-0.749(ws) \qquad (3)$$

with $r_{13} = 0.931$ and $p<0.001$.

It is clear from the estimated correlation coefficients that windspeed is a more significant factor in determining the numbers caught in the trap, but these coefficients alone do not provide the true, independent effects of both windspeed and temperature if they are not totally independent of each other. An inspection of Figure 49a shows that they are related, and the correlation between them, given by r_{23}, is 0.46. In order to estimate the true dependency of catch upon temperature and windspeed, it is necessary to derive the partial regression coefficients, $r_{12\cdot3}$ and $r_{13\cdot2}$ respectively (in this notation, the pair of suffix numbers before the point relates to the variables under comparison, while the number after the point corresponds to the variable specifically excluded from the comparison). The formula for deriving the partial regression coefficients is given as:

$$r_{12\cdot3} = \frac{r_{12} - r_{13} \cdot r_{23}}{\{(1-r_{13}^{2}) - (1-r_{23}^{2})\}^{\frac{1}{2}}}$$

Using the previous calculations, $r_{12\cdot3} = 0.197$ (ln. catch and temperature), and $r_{13\cdot2} = 0.912$ (ln. catch and windspeed). This result provides further evidence that trap catch is predominantly influenced by air movement. However, windspeed along will not account for all of the variation in catch from

night to night, and a bivariate fit for both temperature and windspeed together accounts for a greater percentage of the variance:

$$\ln(\text{catch}) = 0.033 + 0.158(t) - 0.559(ws), \qquad (5)$$

in which r is 0.975 ($r^2 = 0.951$), and $p<0.05$.

Figure 49b shows the ln(catch) expected from the bivariate equation plotted with the actual trap catch, calculated from the measured windspeed and temperature values. Whilst the fit appears close, the reliability of this kind of environmental monitoring is always limited since it is an indirect method of measuring a population.

5.11. The Influence of Meteorological Factors on Airborne Moth Flux

The number of moths passing through a known area in a given time, or flux, can be estimated from the data provided. Using the same analytical procedure as that used for the trap catch, the equation for temperature becomes:

$$\ln(\text{flux}) = 2.55+0.181(t), \qquad (6)$$

with $r_{12} = 0.617$ and $p<0.05$,

and for windspeed:

$$\ln(\text{flux}) = 6.60 - 0.573(ws) \qquad (7)$$

with $r_{13} = 0.939$ and $p<0.001$.

The partial regression coefficient, $r_{12\cdot3}$ for ln(flux) and temperature is 0.607, and for ln(flux) and windspeed ($r_{13\cdot2}$), is 0.938.

This result is very important, as it is clear that the effect of temperature is much more closely linked to the numbers of moths which are airborne in the vicinity of a light trap than to the numbers which are actually caught. Interestingly, the partial regression coefficient $r_{13\cdot2}$ above is little different from the equivalent $r_{13\cdot2}$ calculated for ln.catch (0.938 in comparison to 0.912). The increased importance of temperature implies that a bivariate equation would be of value in accounting for much of the remaining variance, i.e.:

$$\ln(\text{flux}) = 0.071 + 0.344(t) - 0.161(ws), \qquad (8)$$

where r is 0.993 ($r^2 = 0.987$), and $p<0.01$.

The above equation was derived using numbers of moths seen/ unit area/h normalised to $100m^2$. Figure 49cis a plot of ln(flux) overlayed with the expected values, using the measured meteorological parameters. Although at first sight the fit appears to be so close as to be improbable, it is not unreasonable since the method of sampling is a direct one and does not rely upon artifacts to elicit a behavioural change. In the discussion of Chapter One, it was suggested that light-traps suffer from increasing sampling inaccuracy (in relation to aerial moth density), as the windspeed increases. This analysis supports this hypothesis, and it is almost certainly linked to the mechanical problems associated with manoeuvring around a fixed object, relative to the ground, in windy conditions.

5.12. An Estimate of Local Aerial Density

Enough information exists to enable the calculation of local aerial density (for the duration of the sample period), which may be performed in either of two ways:

1) $\left(\frac{\text{nos. seen}}{\text{area x mean airspeed x time}} \right) \times 10^6$

= numbers/10^6 m^3;

2) $\frac{\text{(no. video-fields with insects)} \times 10^6}{\text{total no. of video-fields x sample volume}}$

= numbers/10^6 m^3.

Both of these methods rely on the infra-red detection system as being as "objective" as possible. Taking method one, we know that a good approximation to moth flight speed in calm air for a range of moths is around 1.7m/s (in this case groundspeed = airspeed). Using an area of $100m^2$ and a sample time of 3600 seconds, the density for each night of fieldwork is found to vary from a minimum of 87.41 to a maximum of 1058.01 moths per 10^6 m^3, the latter having been calculated from the data obtained on the 22nd August. Using method (2), from a total of 1.8×10^5 fields, (3600*50), only 4199 contained an image of a moth, i.e. moths were detected in a volume of $25.7m^3$ for 2.33% of the total time. This gives a density of

$$\frac{4199 \times 10^6}{1.8 \times 10^5 \times 25.7},$$

or 907.7 moths/$10^6 m^3$. This agrees quite closely with the density calculated from the first method. On the 31st August, the density given by method (1) is 771 moths/$10^6 m^3$, whereas method (2) gives

$$\frac{3761 \times 10^6}{1.8 \times 10^5 \times 25.7}$$

or 813 moths/10^6 m^3.

Using the density figures of Column 8 , together with temperature and wind data for the respective nights, the bivariate regression becomes

$$\ln(\text{density}) = 0.077 + 0.37(t) - 0.13(ws) \qquad (9)$$

Since the density is a linear multiple of the flux, the r value is still 0.993 ($r^2 = 0.987$), and $p<0.01$.

Unfortunately, the above method suffers from increasing inaccuracy at higher windspeeds since it assumes a constant groundspeed of 1.7m/s; for light windspeeds this is logical, and so methods (1) and (2) agree closely for nights when the mean windspeed was below 1m/s measured at 2m. Observation has shown that in stronger winds moths do not significantly reduce their airspeed, and so the mean groundspeed for a large number of moths is likely to approach 1.7m/s plus the windspeed. This correction has been applied to all detected Lepidoptera, regardless of species.

Although this last assumption cannot be fully justified, neither, given the existing information, can it be disproved. This will of course tend to reduce the density with successively higher windspeeds.

Column 10 of Table 17 gives the density for each night using method (3) - the modified version of method (1), i.e.

$$\frac{\left(\text{nos. seen} \times 10^6\right)}{\text{area} \times (\text{mean airspeed} + \text{windspeed}) \times \text{time}}.$$

The bivariate fit now becomes

$$\ln(\text{density}) = 0.075 + 0.363(t) - 0.423(ws), \qquad (10)$$

with $r = 0.993$ ($r^2 = 0.986$), and $p<0.05$.
Figure 50a depicts actual and expected density for method (1), with Figure 50b repeating this for method (3).

Although this modified version of the density calculation appears almost identical with respect to the correlation and variance coefficients, it is probably a more realistic estimate of the short term effects of temperature and windspeed.

5.13. An Estimate of Trap Effectiveness

The word efficiency is often - and incorrectly - used to denote the magnitude of catch from a light-trap. Taylor and French (1974) point out that efficiency is more properly defined as the success in extracting organisms from the volume that the trap can sample. For instance, a suction trap that extracts 50 times as many insects in one hour as another need not be 50 times as efficient - it may be merely sampling a greater volume of air. The problem is more difficult with estimating the volumetric sample of a light-trap, because it relies upon behavioural and not mechanistic processes for its operation. One method of quantifying the catch rate is to compare the numbers caught per unit time in the trap to the numbers in a given volume of airspace estimated during the period of trapping. This would provide an "equivalent sample volume per unit time", although it would not provide the efficiency as defined above.

To determine this equivalent volumetric sample it is first necessary to carry out a least squares fit upon the estimated density against light-trap catch. The scattergram (Figure 50c) shows the regression line, the linear equation for which is

$$\text{catch} = -1.2 + 0.024(\text{density}) \qquad (11)$$

($r = 0.94$, $p<0.001$).

Thus the trap catches 2.4% of the total number of moths in 10^6 m^3 every hour. This gives an equivalent volumetric sample of 2.4×10^4 m^3/hour. Now the volume of space illuminated by a Robinson trap is approximately hemispherical, giving an equivalent sample radius of 22.62m/h.

This kind of expression is rather confusing as it requires the time of operation to be specified. It is more appropriate to express efficiency as the number of moths extracted from the total flux for a specified area. The regression fit for flux v. numbers caught is

$$\text{catch} = -4.8 + 3.7(\text{flux}), \qquad (12)$$

where flux is in nos/m^2/h
($r = 0.83$, $p<0.002$). See Figure 50d.

The trap catches 3.7% of all moths passing through an area of 100m^2. Assuming that the cross-sectional area of illumination in the vertical plane is $0.5\pi * r^2$, this gives an equivalent sample area of 3.7m^2, with an effective radius of

$$(3.7/0.5\pi)^{\frac{1}{2}} = 1.53\text{m}.$$

This, of course, does not imply that the trap will catch only those moths within that radius; it is merely a convenient form of standardising the catch rate. During the overhead monitoring studies of 1982 for instance, an approximate estimate of flux (taken from the data over 5 nights), was between 50-100 moths/m^2/h in the immediate radius of the trap, yet the total catch was only 12 for 1600 tracks. Most importantly, the flux was much greater over the trap than the flux density elsewhere (as estimated for the following year at the same period) - perhaps by a factor of 50 - and this indicates that the radius of influence may well extend to many tens of metres, although radial densities at this distance would not be noticeably different from the steady background level.

Finally, the light-trap effectiveness (catch/flux) can be calculated from equations (5) and (8). Since this can be expressed in logarithmic form, the constant and slope coefficients of (8) are simply subtracted from the corresponding values in

(5), i.e.

$$\ln \frac{\text{catch}}{\text{flux}} = 0.04-0.18(t)-0.4(w) \qquad (13)$$

If the ratio between catch and flux was constant and therefore independent of meteorological influences, then the temperature and windspeed coefficients would cancel to zero. However, the equation demonstrates that light-traps catch a progressively smaller percentage of the airborne flux as both temperature and windspeed increase. The effect of windspeed is readily understandable from previous analysis, but the effect of temperature is less straightforward (in actuality the errors associated with this kind of manipulation for such a small sample imply that the temperature slope coefficient could be zero or even slightly positive). It is possible, nevertheless, that higher air temperatures allow the moths to fly at an increased speed, aiding them during the escape phase from the trap.

5.14. A Comparison of the Trap Catches in 1981 and 1983

As stated elsewhere, virtually all of the moths caught during 1983 belonged to the Noctuidae. If the total numbers of the four major Noctuid species caught in 1981 are combined for each night, and a logarithmic bivaritate fit is performed for temperature and windspeed, then the expression becomes

$$\ln(\text{catch}) = 0.048 + 0.343(t) - 0.72(w), \qquad (14)$$

where $r = 0.986$ ($r^2 = 0.972$) and $p<0.001$.

Referring to equation (5), the windspeed coefficient is quite similar (0.56 instead of 0.72), and both imply that the catch is approximately halved for every 1m/s increase in windspeed (precisely, the values are 0.96 and 1.24m/s for the catches of 1981 and 1983 respectively). The temperature

coefficients are, however, rather different. These suggest that the catch in 1981 was doubled for every 2°C rise in mean air temperature, whereas in 1983 this value was 4.4°C. It is not likely that this difference represents meaningful information with respect to species composition or other environmental factors unaccounted for, but it can probably be attributed to the smaller sample size in 1983.

The trap effectiveness now becomes

$$\ln \frac{\text{catch}}{\text{flux}} = -0.023 - 0.001(t) - 0.559(w) \qquad (15)$$

(flux is derived from equation (8)). This equation is probably a more reliable estimate of how the effectiveness of a trap changes with temperature and windspeed, than is equation (13).

5.15. Discussion

Taylor and French (1974) use the term "equivalent sample volume" in a somewhat different manner from the above. In their context it is used to define the total volume of possible influence of a light-trap, and has absolute spatial dimensions, independent of time. Bowden (1975) attempted to quantify this volume by stating that the boundary of the region of influence is that distance at which illumination from the trap source equals that from the background (or competitive) illumination. Thus

$$D = (W/I)^{\frac{1}{2}},$$

where W is the trap illumination at a given distance, and I is the background illumination.

Bowden (1982) elaborates upon the above definition by postulating that catch will be similarly affected by increasing

the output power, i.e.

$$\text{Catch} = \text{constant}.(W/I)^{\frac{1}{2}},$$

and under conditions of constant background illumination,

$$\text{Catch} = \text{constant}.\ (W)^{\frac{1}{2}}.$$

Research conducted by Hollingworth and Hartstack (1972) has indeed shown that for many species of moth, catch increases in linear proportion to the square root of the total output power, up to 10,000mW. Bowden and Morris (1975) therefore propose that the effective radius of illumination for a 125W MV lamp ranges from 35m at full moon to 519m at new moon, when the wavelength range from 500-600nm only is considered. Using the volumes calculated from these radii, absolute efficiencies may be derived under differing levels of background illumination.

Defining the volumetric sample in such a manner is perhaps unrealistic; light-traps are not mechanistic (unlike a suction trap), but catch is always probabilistic, the chance of any moth being caught being related in inverse proportion to the distance from the trap - not only is the level of illumination important, but almost certainly the angle of the source subtended at the eye of the insect. Thus distance has its own intrinsic role to play. The findings of Hollingworth and Hartstack may simply be describing the inverse square law in another fashion, but do not necessarily say anything else. Because of this problem, the most meaningful way in which the operation of a light-trap can be described is to compare the catch to the density at the time.

What the present data does show is that light-traps are rather inefficient at extracting moths from the airspace; these findings are by no means unique - of all the moths attracted into an area of $28.88m^2$ around a 15W black-light

Hartstack et al. (1967) estimated that between 10-50% of Heliothis zea were caught, and between 8-38% of Trichpulsia ni. These figures are derived from the numbers of moths sitting on the ground surrounding the light-trap, and although it is not possible to calculate from this the volumetric efficiency, it implies that it is a very small percentage of the numbers within a radius of 519m. Merely because at this point (during new moon) background illumination is equal to illumination from the trap, it does not mean the region of the influence extends this far. Plaut (1971), using mark and recapture techniques, found that with Spodoptera littoralis, the percentage caught when released at various distances from a 15W black-light tube averaged 12% for radii of one to ten metres, but thereafter declined swiftly to 1.4% at 50m and 0.6% at 100m. There is little statistical difference between the last two percentages and Plaut concludes that any moths released at distances greater than 50m are caught by straying into some "sphere of effective attraction" whilst freely roaming.

Although the present studies did not include observations regarding the distance at which significant deviations from an original flight course occur, it would appear that, at least for the trap and species studied, this radius of influence is not greater than 50 or so metres, but changes in flux would not become apparent until much nearer the trap, e.g. 5m. This claim may at first seem improbable, but after examining the catch success in comparison to the flux as calculated, it is not so implausible. Indeed Baker and Sadovy (1978) reckoned the effective range for a 125W MV lamp to be 3m for Noctua pronuba; such a conclusion may appear to be extreme but their experimental method is hard to fault. This involved two independent techniques, both of which produced similar results, but only the first need be described. Four light-traps were placed at the vertices of a square area, at the centre of which was a release point. Initially the traps were positioned at 1m from this point, and so their effective radii overlapped.

This overlapping continued until the distance of any trap from the release point was 4.24m. At this point, all released moths still had to pass within 3m of any trap, and the catch rate did not change from the first setting. Only after this point had been exceeded did the catch rate begin to fall in direct proportion to the "escape area" available. The effective region of influence of a light-trap remains unclear, but it almost certainly falls off more rapidly than some researchers have suggested.

In attempting to gauge this region of influence it is worthwhile to remember that it is not a static quantity. It will inevitably be different for different species and will also be influenced by temporal and environmental parameters. These may operate in a simple mechanistic way, e.g. increasing wind may make it more difficult for moths to enter a trap, or it may be more complex, involving a change in the phototactic state of the organism, such as described by Wilson et al. (1981), who found that the numbers caught in blacklight as compared to pheromone traps for the black cutworm, were greater in summer and autumn than in the spring.

As far as the role wind plays in affecting trap catch, it is now possible to answer the question posed in paragraph (a) of this chapter, at least for the species studied. Increasing wind causes the numbers in flight to decrease exponentially, which is in turn reflected by trap catch. Numerous researchers have demonstrated that for many species, increasing wind adversely affects catch, but few attempts have been made to relate this to aerial populations. The effect of wind is nevertheless not a simple phenomenon. In certain cases, moths actually use the wind as an aid to migration, and will fly regardless of the windspeed. By using radar techniques to study the mass dispersal behaviour of the Spruce Budworm moths over Canadian forestry plantations in New Brunswick, Greenbank, Schaefer and Rainey (1980) revealed that at dusk, spectacular plumes of moths arose

from the tree canopies, initially flying almost vertically upwards until above the calmer boundary layer, whereupon they flew away downwind. The duration of the vertical flight depended upon the conditions of the day, but once the specified layer had been reached, airspeed and groundspeed calculations showed that no attempt was made to fly against the wind - indeed migration would frequently take place between New Brunswick and Prince Edward Island, a flight over sea of some 30km, at heights of between 150 and 300m.

Such a phenomenon is not universal but associated with the behavioural biology of the species concerned. Ideally, R-selected species, characterised by rapid local expansion and exploitation of an environment's resources, require a migratory instinct to ensure the survival of the species. K-selected species, which frequently exist in dynamic equilibrium with their environment (and may therefore be polyphagous) would gain no particular advantage from such large scale organised movement. The species studied at Cranfield almost certainly cannot be classified with such rigidity, but many species on the wing at this time of year are polyphagous and would not benefit from mass-migration. It is probable therefore that the dramatic decrease in catch numbers at 7m is not an artifact arising from vertical displacement to higher altitudes. For pest species (which must be migratory), such as the armyworm (Haggis, 1970), it has been shown that highest numbers have been caught in Kenya when associated with particular wind directions. In Britain, however, Taylor (1974) finds that the aerial density decreases with height, falling off more rapidly for the smaller species. British geometrids for instance decline steeply after even 1m above ground level, whereas for noctuids in an English woodland, density changes little below 10m. In an exposed area such as was sampled in the present work, the density profile is likely to decline with altitude much more rapidly for all species.

5.16. The Use of Imaging Devices in Relation to Pest Management

Until recently the only two options available to lepidopterous pest management schemes for monitoring infestation have been light or pheromone traps; whilst pheromone traps retain the advantages of species specificity, independence from power supplies and frequent maintenance, their efficiency over time is more variable and the catch smaller as compared to light-traps. It is of course impossible to estimate the absolute trap efficiency without some other monitoring device - such as described in this chapter, but although data collected by IR monitoring would have less variance associated with it, it is unlikely to have a great impact on the control of populations if used merely in conjunction with a spray programme; the removal of perhaps 10% of the variance arising from the behavioural changes induced by light, is virtually irrelevant, since pest species typically suffer 95% mortality in the larval stages. For such purposes light-traps are quite adequate, or more realistically, quite inadequate. The benefit of infra-red monitoring can only be realised when the scheme of agriculture, and not the choice of chemical spray, is altered.

CHAPTER SIX

SUMMARY, SUGGESTIONS FOR FURTHER WORK AND CONCLUSION

The work carried out between 1981 and 1983, may be summarised as follows.

1) In 1981 a study was conducted of the nightly and half hourly catch periodicities of four major noctuid species and certain microlepidoptera of the Pyralid family. This work was performed in the late summer using a Robinson trap with a 125W MV lamp mounted at 1.4m and positioned in open cropland.

2) On a nightly basis the most important factors which influenced the catch rate for all species were mean nightly temperature and mean nightly windspeed. The effect of related variables, such as maximum daily or nightly temperatures bore similar relationships, but were never as closely linked to the catch. Humidity was shown to have an indeterminate effect and was dependent upon other weather factors. Illumination from the moon was not shown to have a critical effect on the nightly catch although this was inconclusive as the study did not extend over more than one lunar month.

3) The relationship between catch and temperature (b_1) was not constant, but was different for each of the five species studied. In calm conditions but changing temperatures, the catch reflected the aerial density, and so density was a fuction of both temperature and the range of airborne species.

4) The relationship between catch and temperature is not necessarily a linear one, but for many species is logarithmically linked. By using logarithmic expressions it was possible to find the degree of sensitivity, b_1, associated with the

temperature effect for different sizes and species of moth. No significant correlation over the size range collected was found between b_1 and the tip-to-root winglength, contrary to an expectation that smaller insects are more susceptible to temperature changes. It was also stated that the regression coefficients b_1 and b_2 for a species are representative of the rates of variation of catch about the mean catch level, during a given period in the moths annual flight season.

5) The equivalent coefficient for windspeed, b_2, could not be defined as precisely since the wind exerts several simultaneous influences, with respect to drag and chill. Because of the uncertainty in its relationship with aerial density, light-traps were considered to be less reliable as indicators of Lepidopteran activity in high windspeeds.

6) An analysis was made of the half hourly catch periodicities for different species, and it was found that the smaller species fly earlier in the evening and then decline in numbers more rapidly than the larger noctuids. Since this was interpreted as an attempt to utilise the higher early evening temperatures, it supported the relationship between size and the b_1 coefficient.

7) Note was made of the similarity in the catch periodicity signatures over a single night for N. pronuba and N. Janthina. Although it was suggested that this might have an application as an identification aid, it was also stated that closely related species often have widely different behavioural strategies.

8) In 1982 an image-intensifier coupled to a video monitoring system was used to study the changes which took place in the flight paths of nocturnal Lepidoptera when exposed to a source of high intensity white light focused as a narrow beam, and short distance changes in behavioural strategy which took place around a 125W MV lamp mounted at 5 and 7.1m. Computer analysis necessitated the design and construction of a fast acting light pen and the writing of a software package to process each data field (1/50th

of a second). This provided detailed information on the speeds, accelerations and orientations associated with each track.

9) The results of the narrow beam experiments were studied mainly at a qualitative level, as it was not possible to determine with sufficient accuracy the distance of any track from the source or camera. In nearly all cases, moths were not attracted to the source but displayed an unconditional escape response. This, it was decided, was on account of the dark-adaptation of the visual system, in addition to the presence of an unfamiliar stimulus to which the moths had no suitable response. It was stressed that any behavioural changes must in some way be linked to the concept of adaptive significance.

10) The reactions shown by moths to a 125W MV lamp were quite different to those listed above, due to the universal emission angle when above the plane of the horizontal of the lamp. Because of the physical arrangement of the lamp, it was considerably easier to analyse the tracks on a quantitative level.

11) The time surface matrices produced density distributions using time as the third dimension (along the z-axis), and these indicated where most time was spent in the immediate area around the trap on an hourly basis. They showed that density did not follow a three dimensional Gaussian distribution with the peak centred over the trap, but that the distribution was essentially "doughnut-shaped'. As a result these plots provided the first evidence that phototropotaxis was an inadequate description of the response that moths show towards light.

12) The findings of the time surface matrices were further refined by the calculations on the radial density distributions, which eliminated the disturbances in the density field caused by light winds. These revealed that, taking total numbers of moths flying around the trap, maximum density was attained at a distance of about 40cm from the mid-point of the lamp.

13) The FLITRAP programme examined the dynamic flight strategy of each track event to a resolution of 0.1 seconds, and calculated speeds and accelerations in relation to the time of occurence, distance from the trap and orientation of the moth. These were also linked to the instantaneous wind conditions which were monitored by two vane anemometers with respect to the N/S and W/E vectors.

14) The results produced by this programme corroborated the findings of the time surface matrices and the radial density calculations; they showed that disorientation (which was defined as increased angular velocity and simultaneous positive and negative accelerations) was negatively related to the distance from the trap at which they occured. Furthermore, minimum speeds would take place most often when a moth was flying towards the lamp, and that the converse was often, though less so, true for maximum speeds.

15) Both the radial density plots and the groundspeed distributions showed that a number of overlapping populations were present, having unique dynamic characteristics.

16) The effect of wind was considered to have two distinct phases. Firstly, below 1m/s, the airspeed capability of the moths was not critically affected, and so this had no effect on the distance from the lamp at which moths spent most of their time. Because of their inability to maintain an upwind position, however, the area density was dramatically changed by even light breezes. In addition, it was shown that moths incorporate the wind conditions into their flight strategy, so making vector subtraction an unreliable tool for estimating "intended" behaviour. Thus airspeeds increased in response to increasing windspeed as a result of the time spent in the downwind area of the trap. In higher speeds still, moths were unable to maintain a static position relative to the ground and it is not possible to produce meaningful interpretations of behaviour based on these observations.

17) Some evidence was given to suggest that the density distributions were influenced by competitive sources of illumination, since the distributions were not always perfectly anti-correlated with the mean wind direction. This, however, was circumstantial.

18) The opinion was expressed that the idea of photo-tropotaxis was too general for most purposes. A discussion which included the major hypotheses concerning the influence of light upon moth flight was presented, including the importance of lunar effects and naturally occurring sources of UV radiation.

19) An account was given of the Mazokhin-Porshnyakov hypothesis which states that moths fly towards light because they mistakenly associate the UV wavelengths as indicating open sky. Since the major source of this UV at night is the moon, this hypothesis could accommodate the lunar theory of moth attraction towards light. The overall hypothesis was in need of some elaboration however, since it assumed an overall

attractive response and could not account for moths which are not caught by light traps, but merely disorientated.

20) The elaborated Mazokhin-Porshnyakov hypothesis was proposed as an explanation for the observations of the 1982 data. It was founded not only upon a misappropriately applied attraction response R_a, which operates over long distance, but also upon a short distance escape response R_e. This latter response only begins to operate when visual clues indicate that the source is not what it was originally considered to have been. R_e is linked to the unconditional escape response that moths exhibit upon exposure to a narrow beam, but in this case the behaviour arises from a combination of R_a and R_e, leading to disorientation. Two time constants operate, one to extinguish either R_a or R_e, so that the moth subsequently escapes or is caught, and the second determines the time necessary for the re-establishment of the extinguished response.

21) The hypothesis was discussed at a quantitative level and an equation derived which described the ideal density distribution in calm air and in light windspeeds below 1m/s. The distribution was further a function of the cosine response relative to the angle of the wind, but the distance at which the peak density occured was independent of the wind if it remained below the critical threshold.

22) The equation could not adequately describe the density changes in response to higher windspeeds due to a shift in the distance of the peak. This could only be accommodated by changing the values of the R_a and R_e components, but since they represented behaviour and not environmental dependency, it was not a valid modification of the equation.

23) In 1983 a calibration of a light-trap was attempted, which also linked the 1981 and 1982 work. Two 125W MV Robinson traps were placed at 1.4m and 7.1m and during the time of operation a known volume of air was monitored by the use of an infra-red beam and an image intensifier.

24) The low catch rate of the trap mounted at 7.1m indicated that the catch pattern of 1982 was not atypical, thus safeguarding the analysis.

25) On a short term basis, the total number of moths caught in the 1.4m trap was best described using a logarithmic bivariate fit of mean temperature and windspeed.

26) The aerial density was calculated using two separate methods and both produced very similar results.

27) The bivariate fits of(25) were much more reliable when applied to flux and density changes as detected by the monitoring system, as it represented a direct method of sampling the activity of the moths.

28) The effect of windspeed upon density was discussed in its relation to mass-migratory and non mass-migratory species.

29) The calibration of the trap was expressed in two forms: firstly as catch per unit time versus density during that time, and secondly catch versus flux.

30) A discussion was presented on the work which has been done regarding trapping efficiency. It was suggested that defining the effective sampling volume of a light-trap was too artificial to have any practical use, and that catch was best expressed in relation to density or flux.

31) Judging from the three years' work, light-traps were considered to be rather inefficient at extracting moths from the environment, even those using high output UV sources. This was especially true for traps operating in exposed areas and not in enclosed woodland or suburban gardens. With respect to pest management, it should be understood that a low adult catch does not necessarily imply a low infestation in the next generation period, due to the mortality rate of the larval stages.

Suggestions for Further Work

It is always easy with the knowledge of highsight to suggest ways in which the work might havebeen improved. In the present case, more could have been accomplished if time had been available and certain problems associated with eliminating unwanted data could have been overcome.

The b_1 and b_2 coefficients derived in 1981 could be tested and extended in two ways; as temporally invariant coefficients, they should remain the same for any species over a number of years. Similarly, they should be roughly the same for different species of the same size living in similar climates. Secondly, the slope describing the linear relationship between wing length and b_1 could be placed on a firmer foundation by testing it for species having a winglength much greater than the range set by N.Pronuba and A.trisella. Because only five species were studied in detail, it was uncertain whether (as suggested) the catch periodicity signatures were indeed similar for closely related species. To study this in depth would require great dedication on the part of the researcher, but the results may well prove worthwhile.

One of the more elaborate ways in which this work could be extended would be to study the variability of the b_1 and b_2 coefficients in different climates, perhaps in the tropics where the temperatures are much higher than those in Britain.

As far as is known, the work performed in 1982 was the first of its kind to be attempted and so a whole range of possibilities are available to improve and refine the analysis. The escape response shown by moths when encountering a beam was not studied in a quantitative manner, but by altering the physical lay-out of the equipment the precise distances at which moths entered the beam could be established and the data could be processed in a manner similar to that of the overhead work. In addition, the types of track encountered could be related to different frequencies and intensities of emission, as well as to different angles of beam spread.

One of the problems with this kind of work is that if a number of species are present having similar wing and body dimensions (as do many of the noctuids), then it is not possible to separate out these species by merely observing the video recorded images. The fact that overlapping populations were present gives a tantalising glimpse of what might be possible if individual species could be studied in isolation. The only way in which to achieve this would be to position the apparatus in an area where on species predominated as a result of the surrounding vegetation. This would not be easy to do in Britain, as there are no major pestiferous species of moth associated with agriculture. This could be done in other countries however, and a set of radial density distributions could be plotted for a number of species.

The particular aspect of radial density distributions holds fascinating possibilities in the field of phototactic research. It was mentioned in Chapter Four that the reason why each species has its own preferred radial density is because it is linked to the way it has adapted to its environmental niche. It is therefore logical that a close relationship exists between the flight periodicities and the radial density distributions.

As regards the quantitative aspects of the equation describing the elaborated Mazokhin-Porshnyakov hypothesis, this could be defined more precisely if a single species was available for a detailed study. It would be interesting to discover whether the general form of the density distribution was different at mid-summer, since the work was performed towards autumn. As it stands, the equation cannot be applied in conditions of high windspeed, and for this to be possible, a much longer period of sampling in different weather conditions would be necessary.

No analysis has been made of wingbeat frequencies, although this would certainly have been possible with the present data. Again, if species identification was possible, wingbeat frequencies could have a use as an identification aid. Further analysis could be done on this topic with respect to speed changes, weather conditions and forms of illumination.

The only major improvement of the fieldwork set up would be with the use of a second camera, as this would allow the vertical movements to be quantified. The computer programmes involved with the data analysis proved satisfactory, and any modifications here would be of minor importance. Although the light-pen was adequate in its function, the two stage process in first producing the voltages corresponding to the x and y position, and then converting these into a form acceptable to the computer could be combined by the construction of a digital light-pen.

The 1983 calibration work could be made more accurate by extending it over time and limiting it to certain species. This calibration was only applied to a Robinson trap, but the same method could be used to calibrate other commonly used designs such as the Rothamsted 200W tungsten filament trap. It is certain that the aerial density changes with height, and a study to this effect would be most useful.

Conclusion

The value of a piece of scientific research is often decided by its potential for application. The intention of this work was to highlight the enormous complexity of some aspects of insect behaviour, and from this point of view it was not an academic exercise. If we are better able to understand the way in which the whole of nature is interdependent, then we are better equipped to live in harmony with it.

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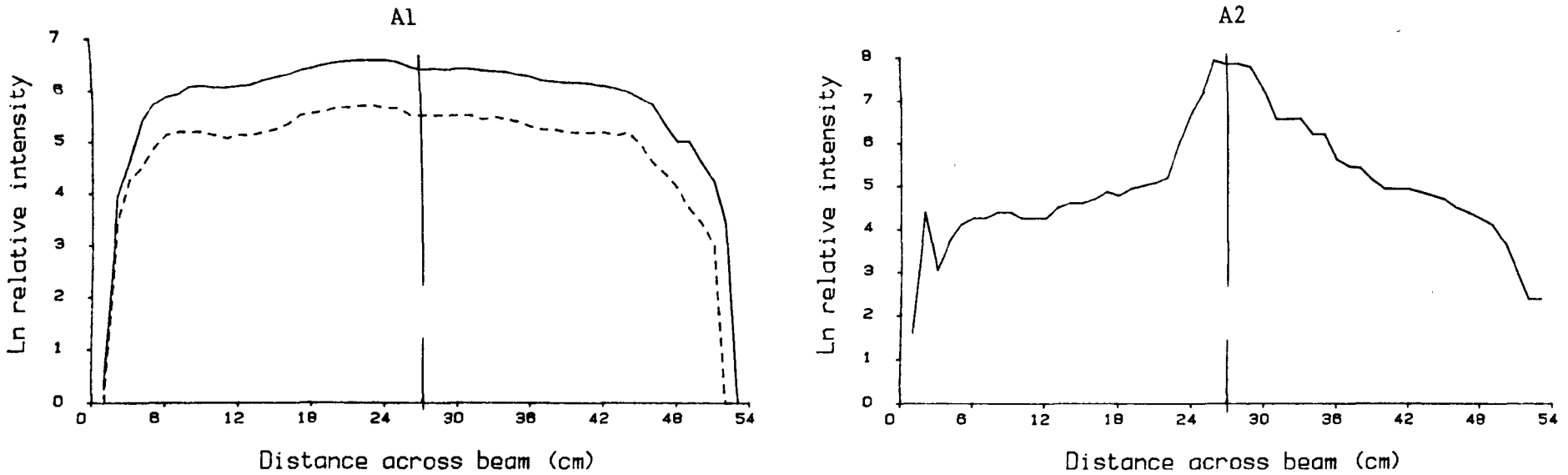
APPENDIX A

Output Characteristics of the Quartz-Halogen Narrow-Beam Source

This apparatus was designed to emit a beam of light with a sharply defined cross-sectional irradiance, uniform across the angular width of emission. This uniformity remained constant between 4^{o} and 15^{o}. Figure A1 illustrates the Log (natural) relative irradiance measured at 2.86m by an RS 305-462 photodiode which outputs a leakage current linearly related to the incident energy ($\mu W/cm^2$).

The edge of the beam was defined as that distance (from the centre) at which the measured irradiance had fallen to 1% of its maximum value. The curve obtained from the unfiltered output contrasts sharply with the curve obtained from the output of an unfiltered tungsten bulb focused by means of a 6cm wide parabolic reflector, measured in the same manner (Figure A2). Because of its non-uniformity (the beam angle of which was again defined by the 1% power points), the volume of illumination is "soft-edged" and is therefore unsuitable for aerial moth density calibration purposes.

The quartz-hologen tungsten lamp used in the above device (12V/50W) operated at a colour temperature of 3270K (see Figure A4), unlike standard tungsten lamps which operate at a colour temperature of between 1800 and 2500K.



All readings taken at 2.86m

Cross-sectional irradiance profiles for:

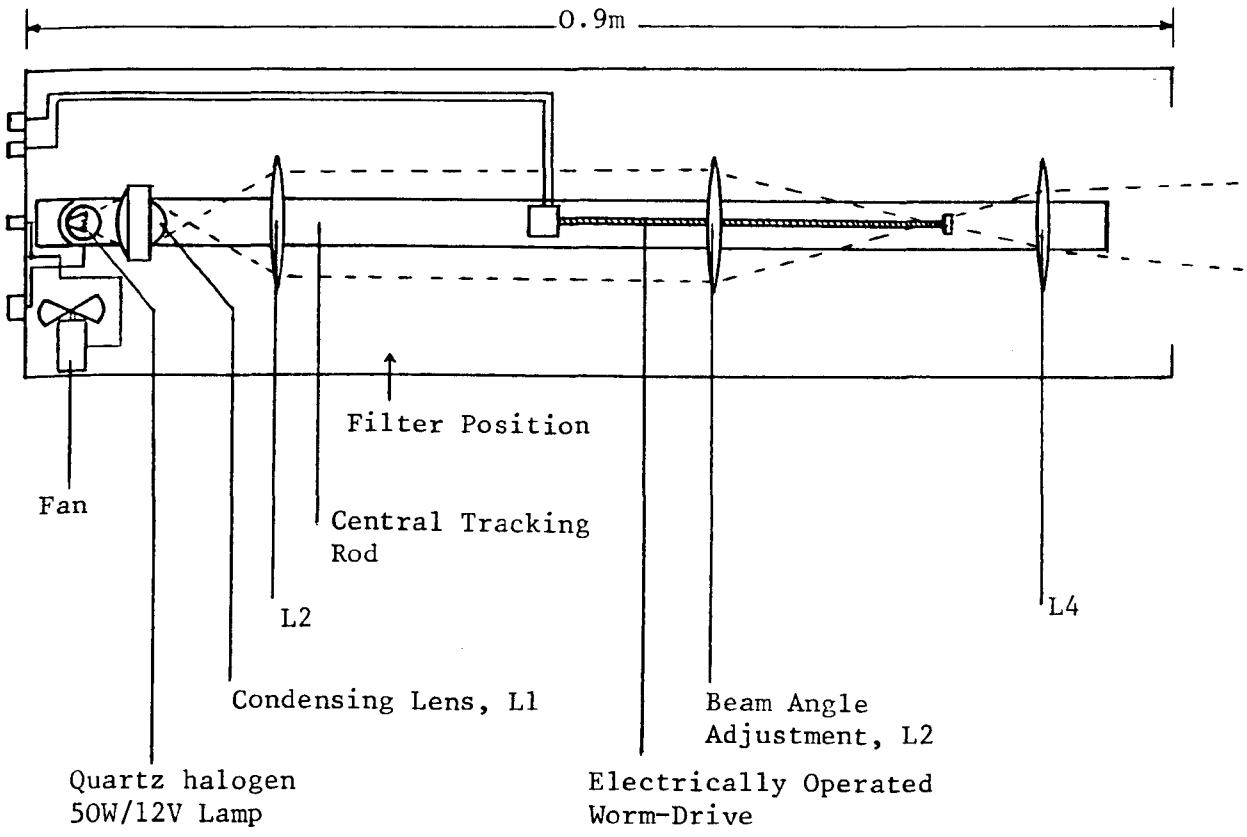
A1) narrow-beam quartz-halogen source (see text), and

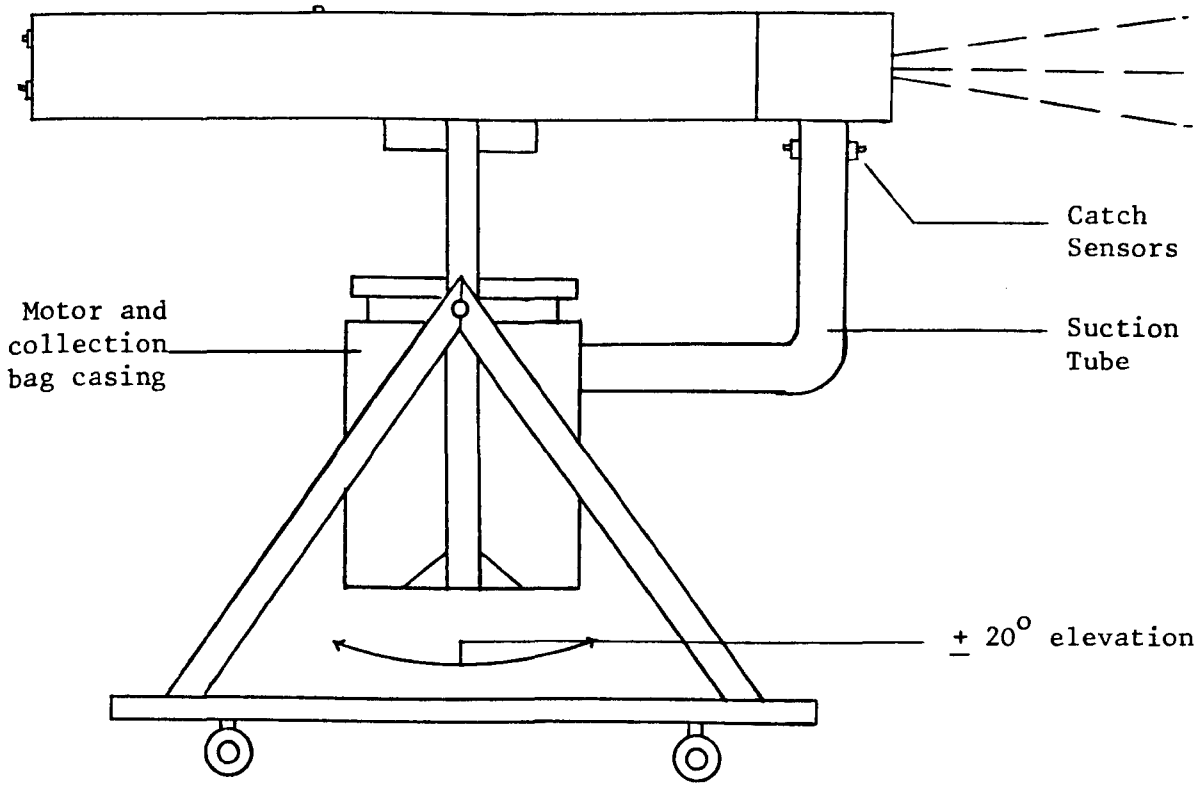
A2) torch parabolic reflector.

Dashed line of (A1) indicates the same device fitted with an RG780 filter.

1% power-points for (A1) (unfiltered) and (A2) are 2.1 and 3.4 respectively.

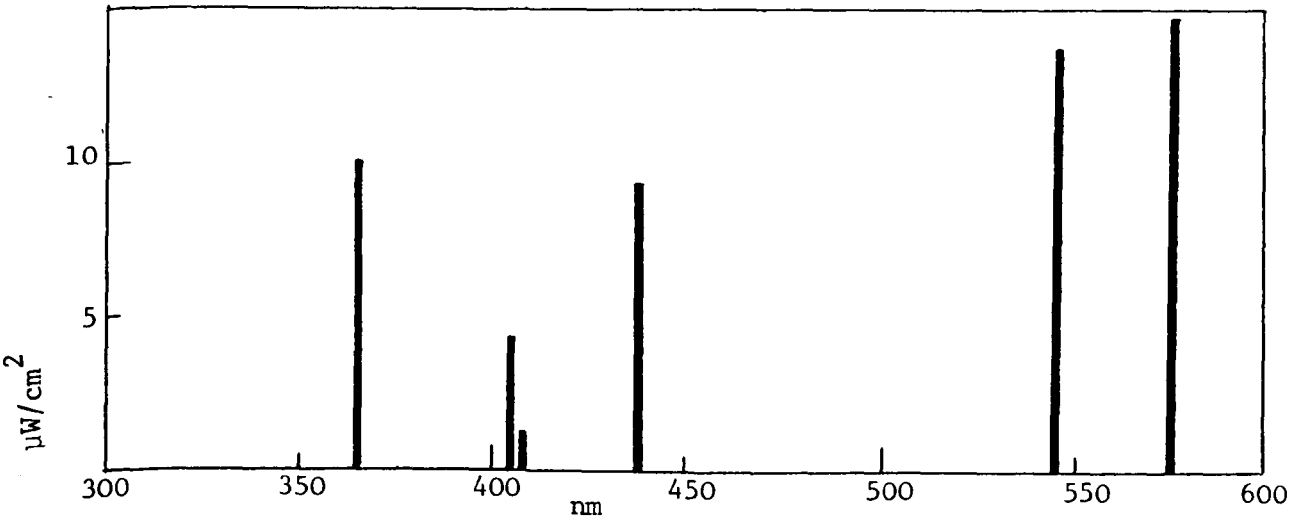
Figure A1 & A2



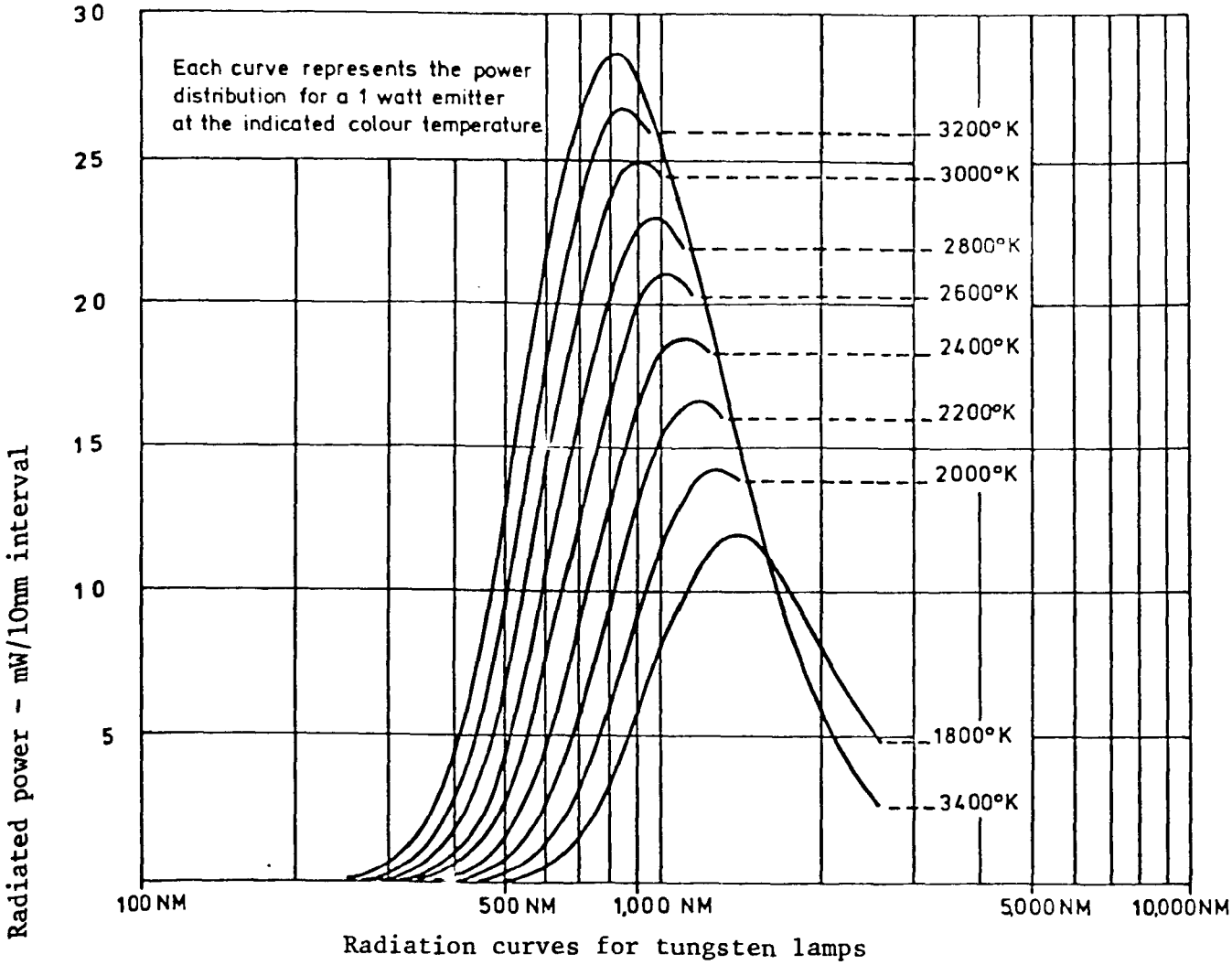


Narrow Beam Source and Mounting Hardware

Figure A3



Spectral emission from Low-pressure Mercury vapour lamp, 125W (Philips HP2 125W), measured at 1m.



Radiation curves for tungsten lamps

Operational range: 1800-2500K, vacuum tungsten
2500-3400K, quartz-halogen-tungsten

Spectral emission curves for MV and tungsten lamps Fig. A4

APPENDIX B

Construction and Use of the Lightpen

Introduction

The purpose of this device is to enable the direct transfer of co-ordinates seen on the surface of an independent monitor screen to a computer, to be stored in memory or to be displayed on its own visual display unit. See Plate 2.

Circuit Theory

Each field of a T.V. picture, operating at 50Hz, is produced by a fast moving electron beam which scans rapidly across and down the face of the cathode ray tube. Although 625 horizontal lines is the standard accepted in the UK, only 312.5 lines are scanned each 1/50th of a second, but these fields are slightly displaced and interwoven with each other to produce a complete frame every 1/25th of a second, resulting in what is called an interlaced image.

The electron beam is controlled in its movement by the cathode ray tube's x and y plates, which have a linearly changing voltage applied to them (i.e. a ramp voltage), pulling the beam from left to right in 64 microseconds (0.02/312.5) and from top to bottom in 0.02 seconds.

Essentially, the light-pen circuitry takes the trigger pulses for these ramps (the x from the monitor and the y from the video tape recorder), and uses them to trigger its own more linear ramps (standard T.V. ramp voltages are slightly curved to accommodate a slightly curving screen). When the light-pen is placed at any position on the screen, a light sensitive photodiode is activated as the beam crosses its face, generating a voltage spike which instructs the circuitry to sample the x and y voltage ramps at that moment in time. Because the ramps of the light-pen are synchronised to those of

the monitor, the voltages taken from the two ramps correspond to the position pointed at by the pen (see Figures B1 and B2).

Circuit Description

The accuracy of the system is critically dependent upon the response time of the photodiode used in the tip of the light-pen, i.e. to ensure an accuracy of 1%, the detectable rise time of this sensor should not be more than 640 nanoseconds. The photodiode used was an RS 305-462, connected in the photoleakage mode and having a maximum output of a 1mA, depending on the strength of the received signal (see circuit diagram, Figure B3). This is connected to a preamplifier stage contained in a screened box within the light-pen casing. The preamplifier uses a pnp-npn complementary pair generating a signal gain of:

$$Ra/Rb = 3300/15 = 220.$$

The output of this pair is fed to the input of a 311 comparator, which is set to trigger at 15mV by the potential divider network. The rise time of the output is less than 100 nanoseconds ensuring an accuracy to within 0.15%. Waveform 1 of Figure B4 shows the output signal from the preamplifier.

The sampling of the two linear ramps is performed by two sampe-and-hold devices (LM398), and in order for them to sample long enough for the A/D converter to operate a full conversion, the signal from the preamplifier must be altered to a waveform of constant and longer duration - in this case 2mS was found to be adequate. This is achieved by a 555 timer connected for monostable operation, which triggers on an amplified copy of the preamplified signal. This amplification is provided by a two stage transistor circuit (2N2904 and BC107) whose output waveforms are labelled 2, 3 and 4 respectively.

The 555 timer produces a signal shown by waveform 5, which is used both to trigger the A/D converter and the sample-and-hold circuits. In the latter case the amplitude is reduced from 14V peak-to-peak to around 1V, since 398s function more reliably on small trigger voltages.

The sample-and-hold devices are, unless triggered, connected so as to constantly 'track' the output from the linear ramp circuits, and hold the voltages corresponding to the light-pen's position only when instructed to do so by the rising edge of the trigger pulse.

The linear voltage ramps are generated by using two additional 555 timers, the timing being controlled by the x (line) and y (frame) synchronisation signals as previously stated. Linearity is achieved (waveforms 8 and 11) by replacing the pullup resistor normally used in the monostable mode with a constant current source, a pnp transistor. This causes the timing capacitor to charge up linearly with respect to the voltage at pin 6 of the timer. If a bias current is applied to the transistor by a potential divider network R1 and R2, with a load resistor R1 charging a capacitor C, then the timing interval is given by:

$$T = \frac{0.67VccR1\ (R1 + R2)C}{R1Vcc-Vbe\ (R1 + R2)}$$

Where Vcc is the supply voltage and

Vbe is the voltage drop across the base-emitter junction (approximately 0.6V). By choosing suitable values for these components, timing cycles of 50Hz and 15.625KHz were produced, as shown by waveforms 8 and 11. The outputs from the sample-and-hold-circuits are shown by waveforms 9 and 12. The trigger pulse (5) matches the hold state with respect to time of occurence and duration.

Operating the System

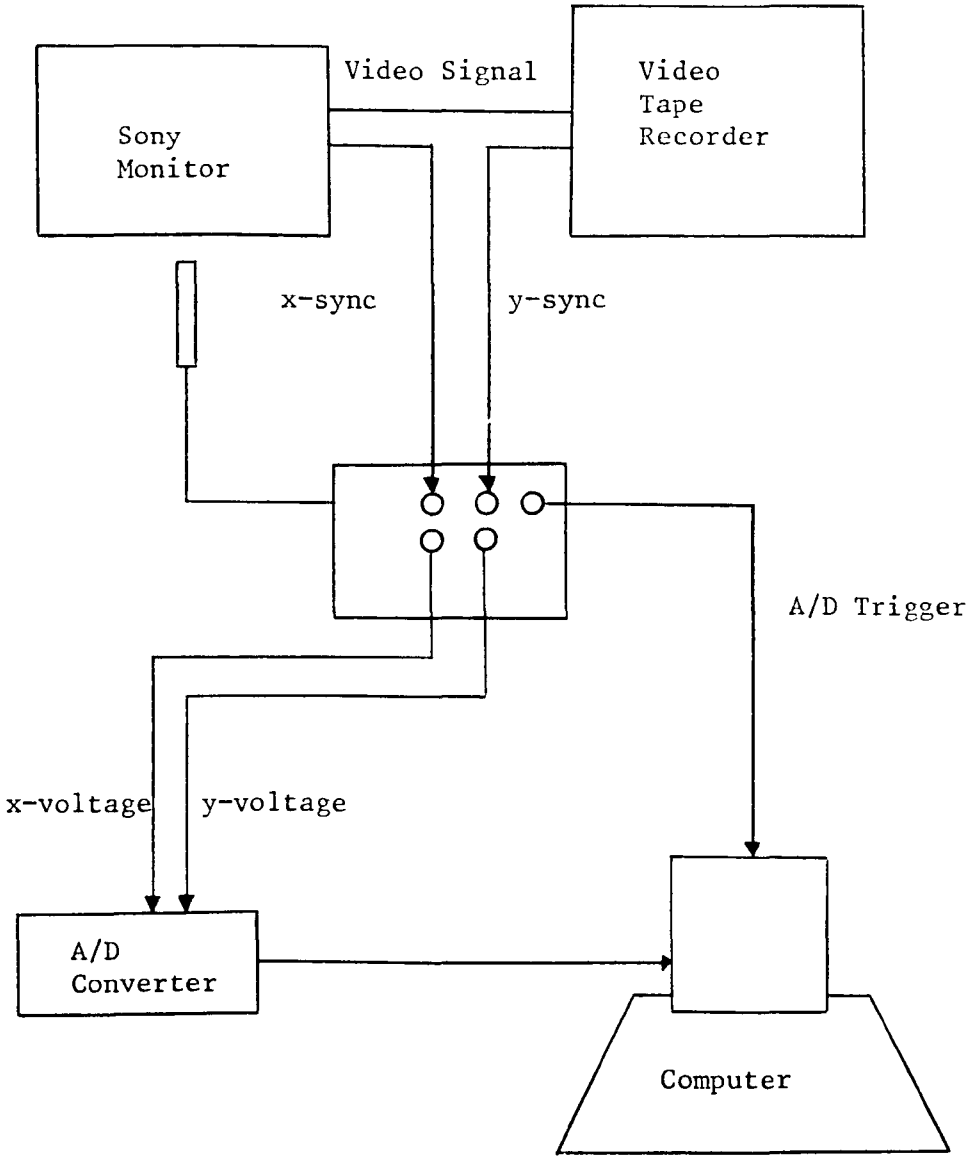
The light-pen is connected to any suitable ±15V power supply, and the mid-point used as the ground rail. The x-sync BNC socket on the front panel of the casing is connected to the equivalent socket located on the rear panel of the modified Sony T.V. monitor, and the y-sync socket is connected to the 50Hz sync signal coming from the video tape recorder. The trigger output is then connected to the J2 connector of the A/D motherboard within the Apple computer (refer to the A/D manual), with the signal lead nearest to the front of the machine. X-out and y-out are now connected to any two channels of the A/D converter - in this case channels 0 and 1 were used. All that is now required is a programme to read the voltages and convert them to useful magnitudes.

Calibration of the Voltage Signals

The range of the voltage ramps is 0 to 10V, although only a part of this is used in the case of the y-ramp since the screen is rectangular. Once the voltages have been read off, any suitable scaling may be used (the conversion chosen corresponded to the Apple's screen size). In practice it was found that the lower values of the x co-ordinates exhibited a slight non-linearity due to the increased speed of the electron beam sweep rate when close to the left-hand side of the screen. Fortunately this non-linearity could be corrected by the following derived formula:

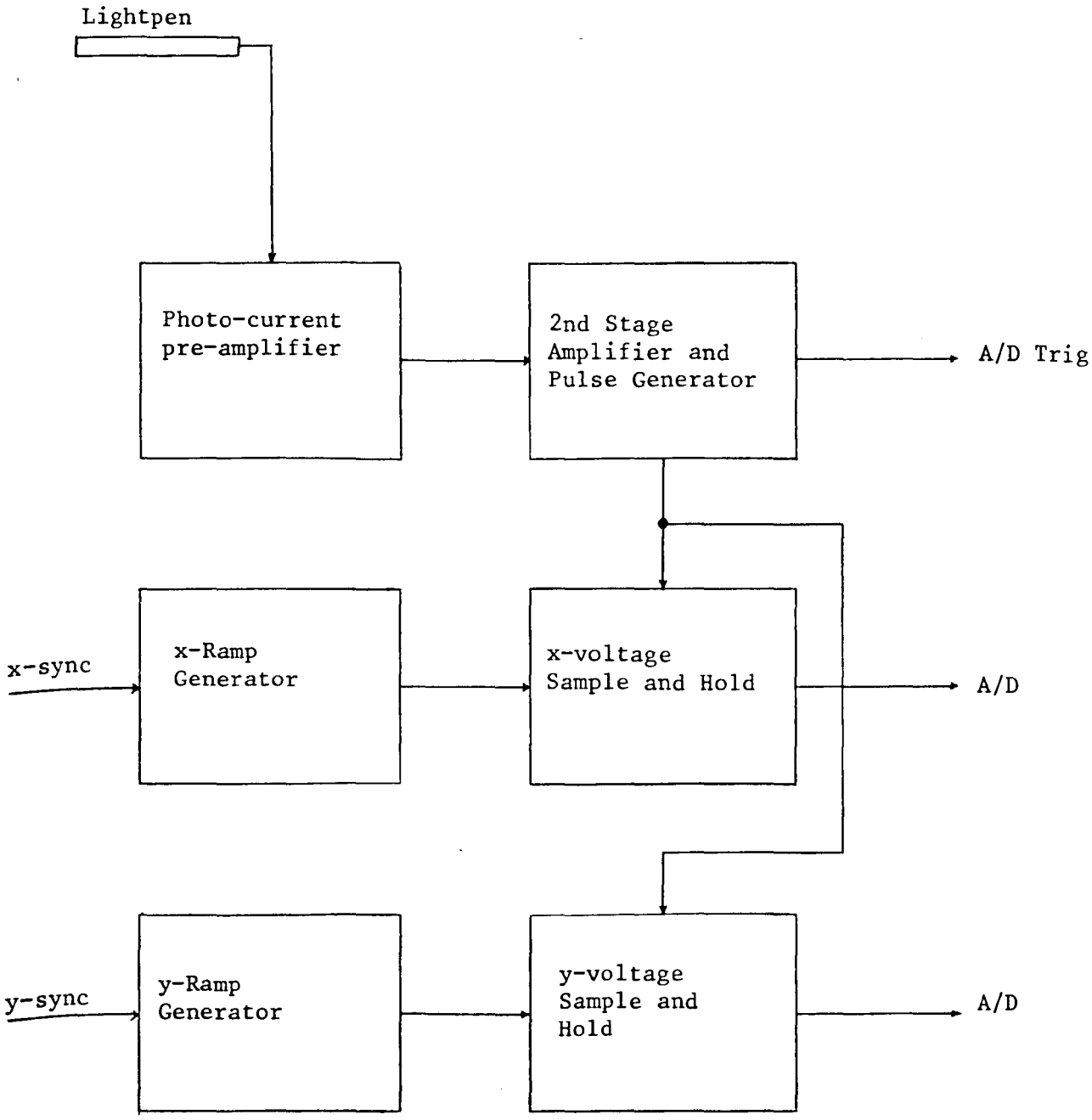
$$x2 = (4.53 \times x1^{0.691}) - 17.31$$

where x2 is the new value calculated from x1. This correction was only found to be necessary for those x co-ordinates below 50 screen units.



Lightpen System

Figure B1



Schematic Diagram of Lightpen Circuit Operation

Figure B2

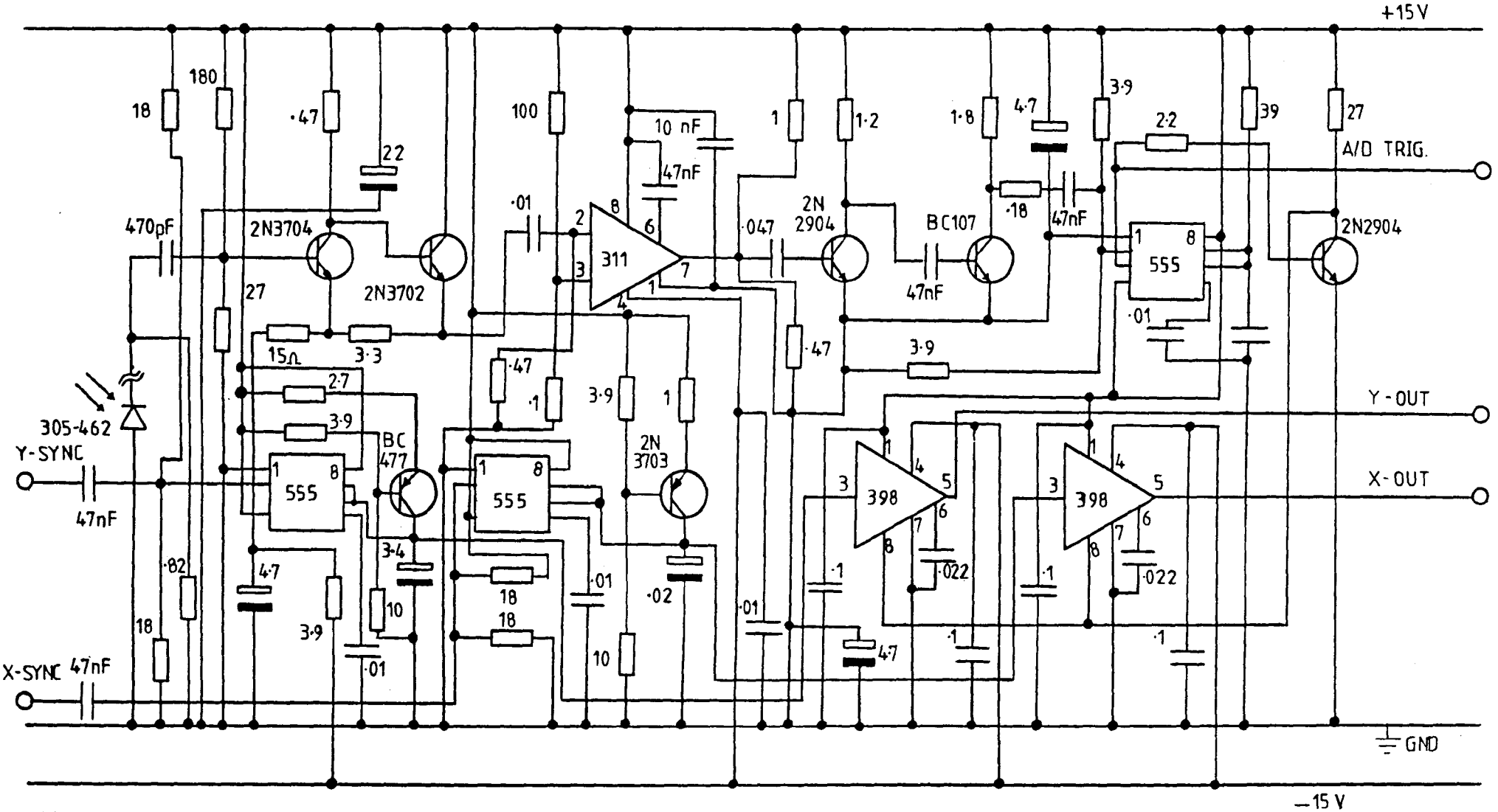
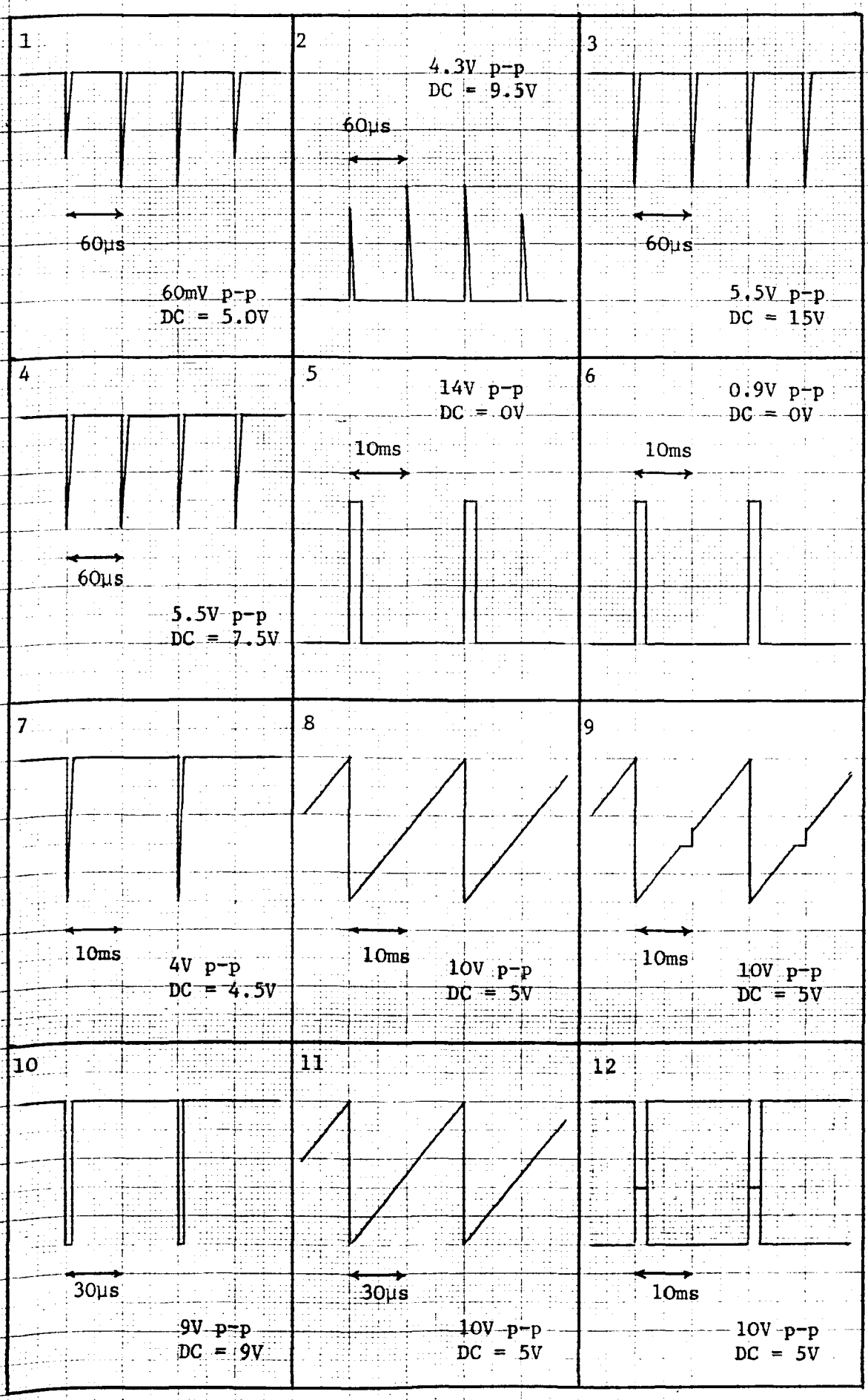


Figure B3

Lightpen Circuit Diagram

All resistances in KΩ and all capacitances in μF unless otherwise stated.
Figures in Red denote wave-form test points



Waveform test points of Light-pen circuit Fig. B4

APPENDIX C

The Construction and Use of the TTL Data Converter and sync-separater as applied to the Digital Anemometer Processor

This item of equipment functions by taking both synchronisation and data signals generated by the anemometer processor (or its tape recorded equivalent), and performs the following:

a) separation of the multiplexed block and bit sync pulses;

b) amplification of both sync and data pulses from 1V to 5V, making them TTL compatible.

Synchronisation Pulses

These pulses are multiplexed and consist of one positive going block pulse for every 100 negative going bit pulses (see Figure C1). Referring to the circuit diagram given by Figure C3, after the incoming sync pulses have passed through the decoupling capacitor and the potential divider network, all pulses become positive, with the bit sync pulses ranging from 0.5V to 1.5V and the block pulses from 1.5V to 2.5V. Comparator one is set to trigger when the voltage at pin 2 rises above 1V, and so produces a 5V square wave in synchrony with the bit pulses. Comparator 2 is set to trigger at 2V, and will therefore only produc a 5V pulse on reception of the block sync signal. In this manner, comparators 1 and 2 separate out and amplify the incoming multiplexed signals. Figure C2 show these new waveforms.

Data Pulses

Figure C1 also gives the data signals which have a positive range from 0 to 1 volt. Comparator 3 simply amplifies these signals to 5V by triggering on a 0.5V threshold at pin 2, represented by Figure C2.

The manner in which the information is multiplexed from a maximum of 12 anemometers and then separated out into meaningful values to correspond to a measured windspeed is beyond the purpose of this thesis, and in any case is clearly described by Bent (1982), Pinnock (1983), and Scannell (1984).

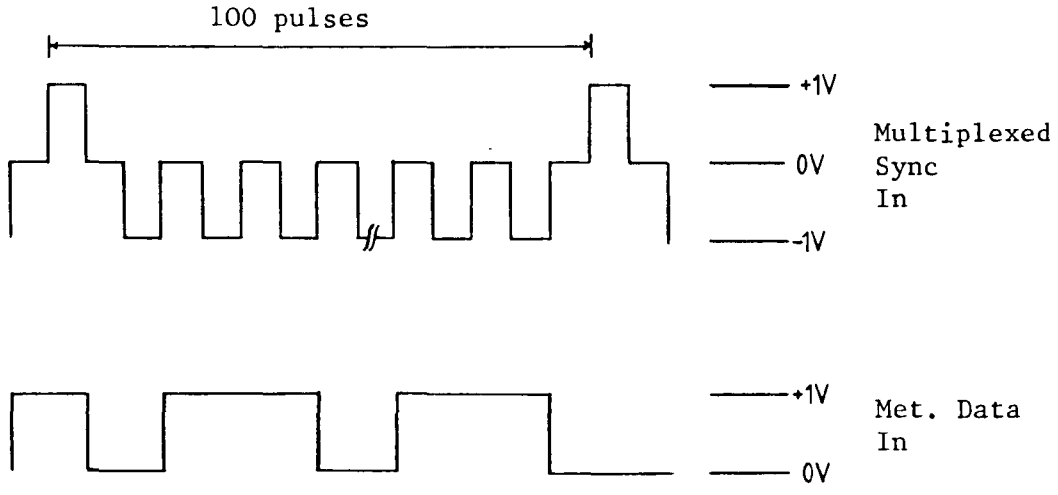


Figure C1

Output of meteorological processor

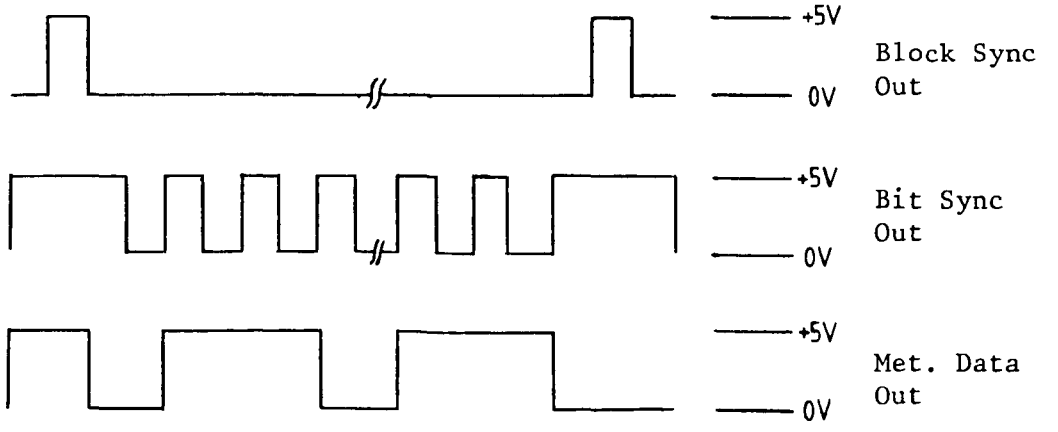


Figure C2

Decoded output of meteorological processor

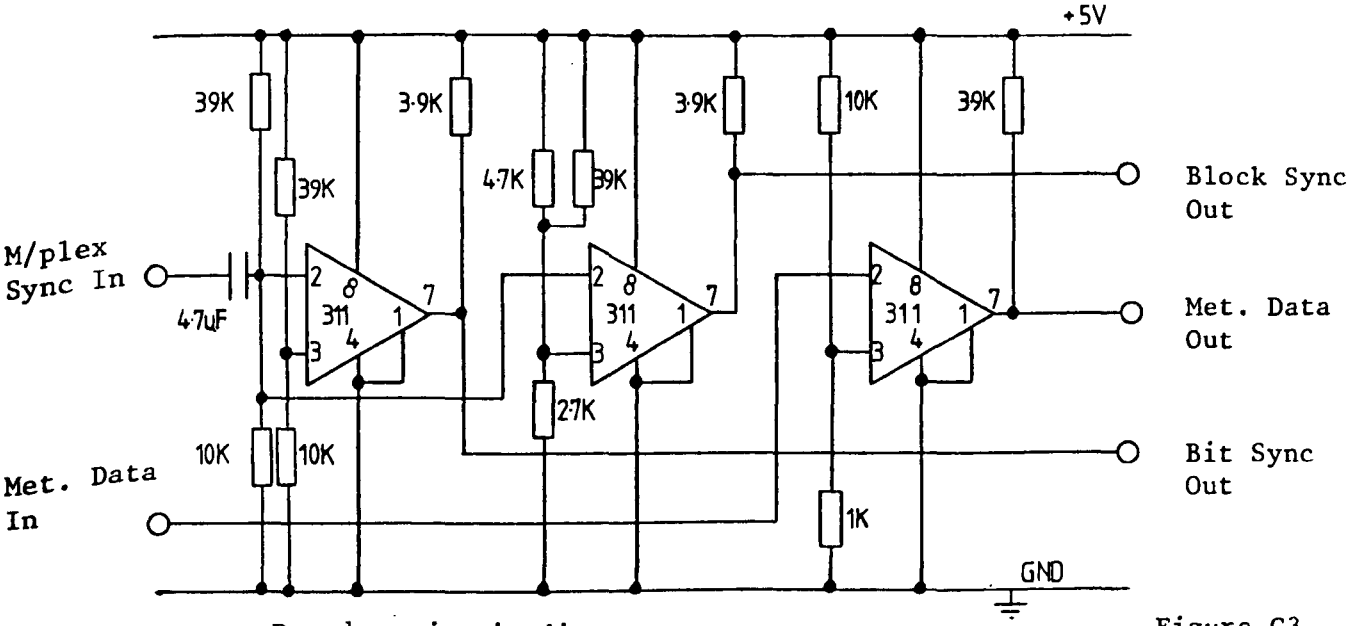


Figure C3

Decoder circuit diagram

APPENDIX D

Moths Captured, 1982 and 1983 Field Seasons

Table D1 - 1982 Figures for MV125W Elevated Trap

Species	Dates in September				
	6	8	9	10	11
N. pronuba	1				1
D. rubi	1				
X. aurago	1				
X. c-nigrum		2		1	
M. impura		2	1		
A. tragopogonis				1	
P. meticulosa					1

Table D2 - 1983 Figures for Traps at Two Heights (MV125W Robinson Type)

N.B. Figures in brackets denote catch at 7.1m.
All else at 1.4m.

Species	Dates in August									
	19	20	21	22	24	26	27	29	30	31
P. meticulosa										
D. rubi	1	1	1			2	2	1	1	3
X. c-nigrum			3(1)	8(1)		3	1		4	3
P. fuliginosa	1		1	2(1)						
M. secalis		1	3	7(1)		1			1	
H. sylvina			(1)							
N. pronuba			1	3		1			2	3
E. ochroleuca			1	(1)						
L. testacea				(1)						
X. xanthographa				1(1)						
A. monogylpha				1						
M. pallens						1	1			
N. comes										1
M. impura										1
O. plecta										1
A. tragopogonis	1			(2)						1
Unidentified	1		1	4						2

ACKNOWLEDGEMENTS

I should like to thank, in no particular order, the following people. Pam, for the superb work she has done in typing and crafting the layout of this thesis. Terry, for many enlightening discussions on moth habits and behaviour. Lynne, for guidance in some of the more theoretical aspects of biology, and help during the calibration work of 1983. My Supervisor, Professor Schaefer, without whose advice and assistance this thesis would not have been possible. Dave, for his help during the construction of the lightpen. Brian, Keith and Steve for useful advice in the mathematical areas. I should also like to mention my family.

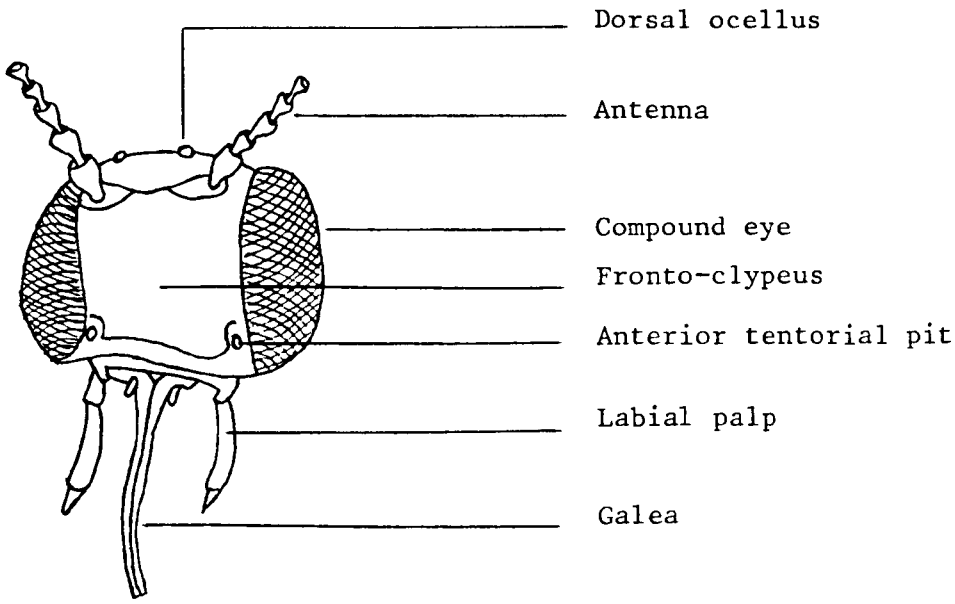
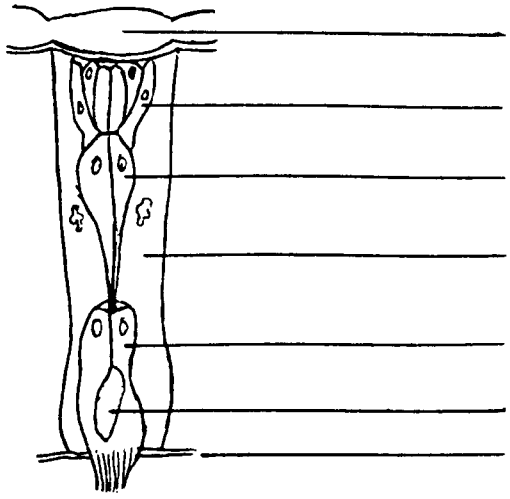
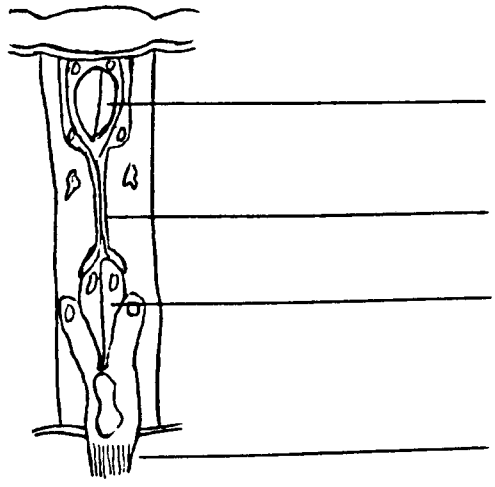


Fig. 1a. Head of Lepidoptera - Frontal view

(b) Dark-adapted



(c) Light-adapted



Figs. 1b and 1c. Histology of an ommatidium

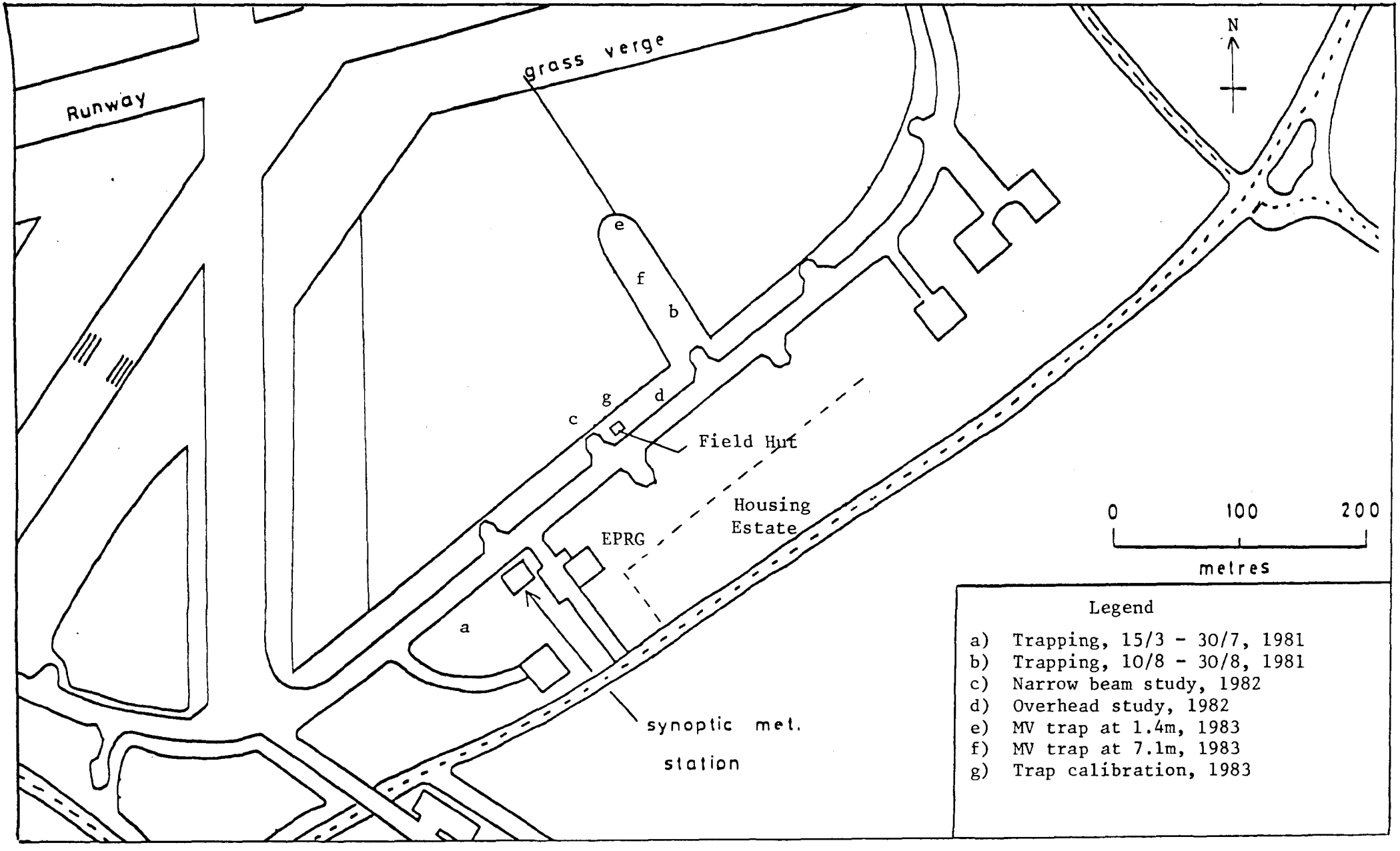


Fig. 2 Fieldwork sites, 1981-1983

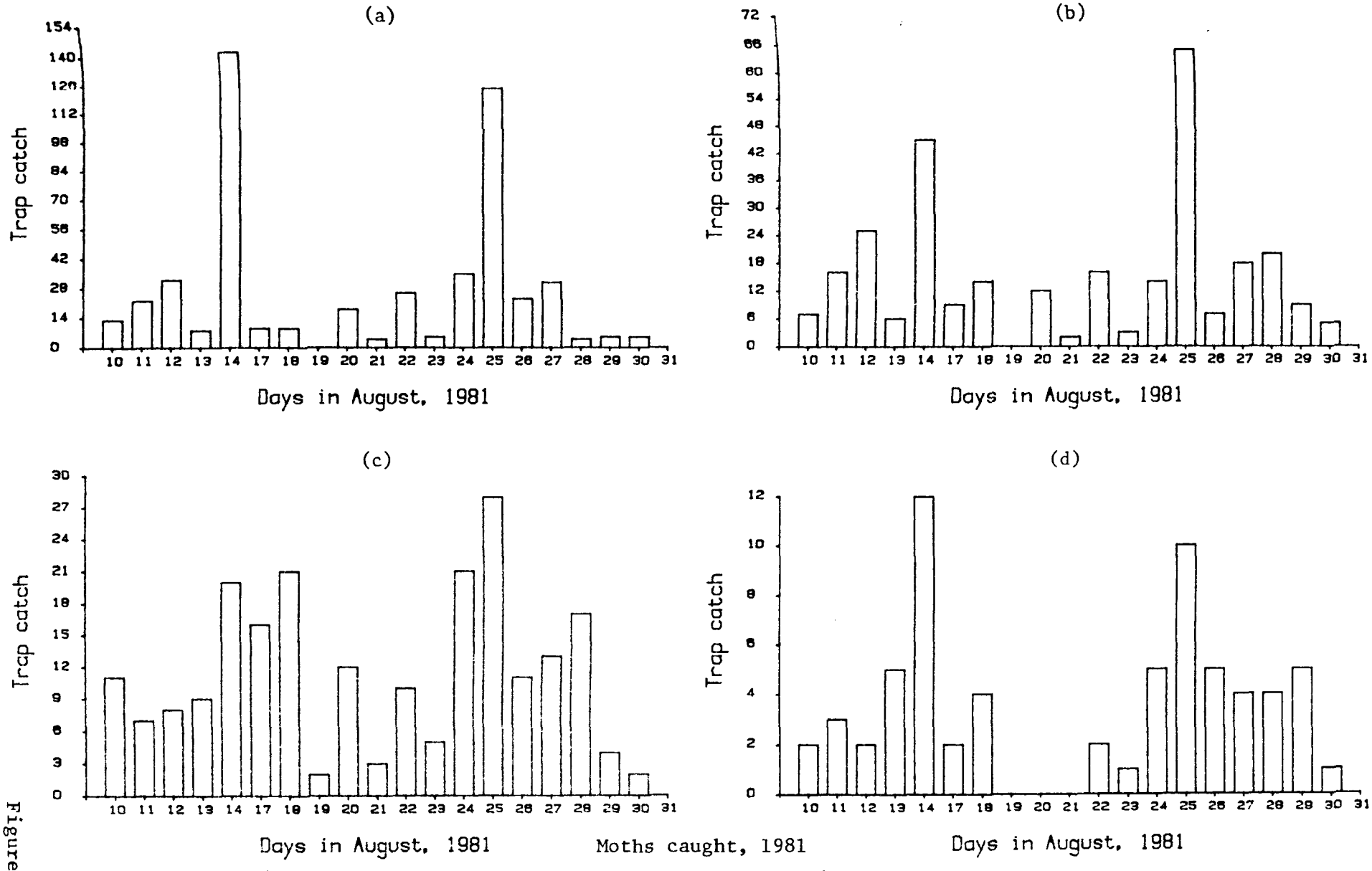


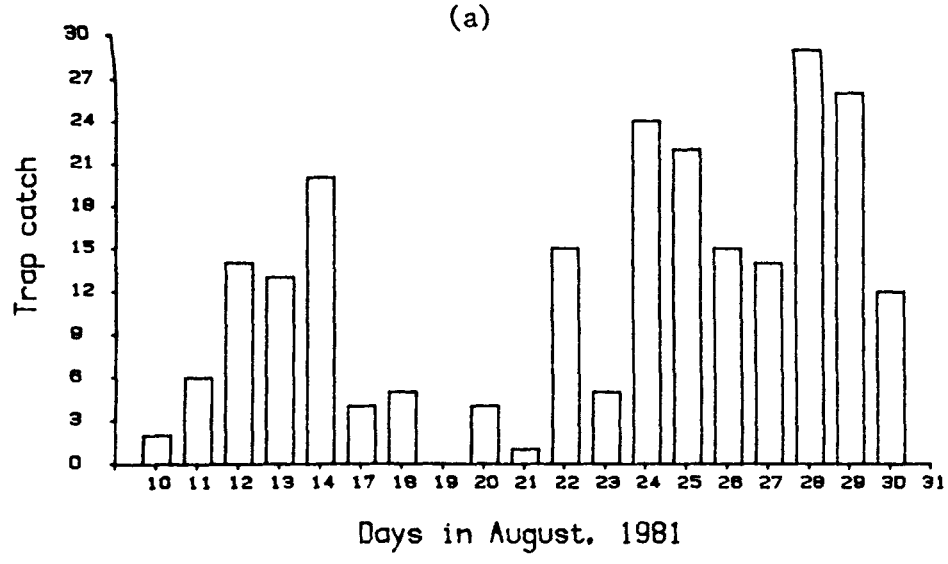
Figure 3 Moths caught, 1981

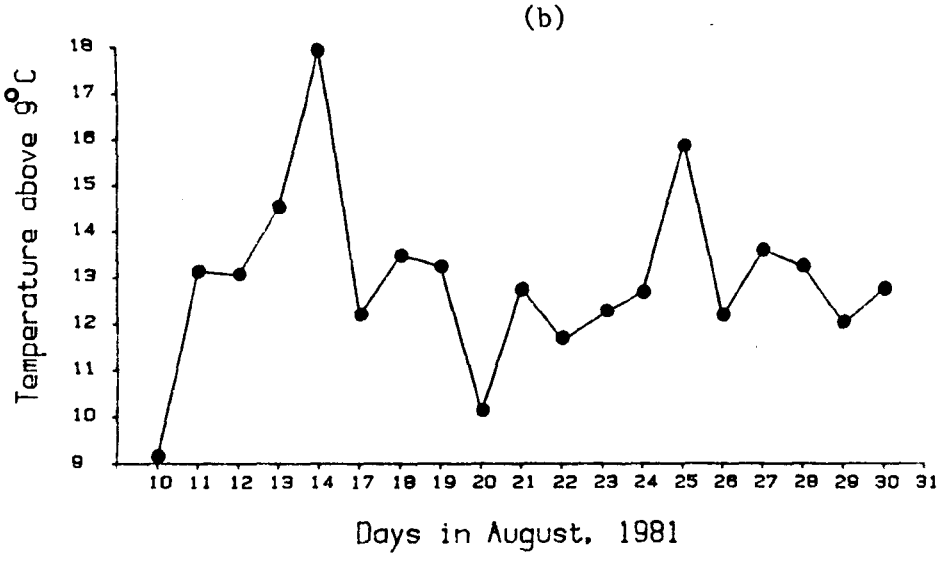
a) Pyralidae (mostly A. tristella)

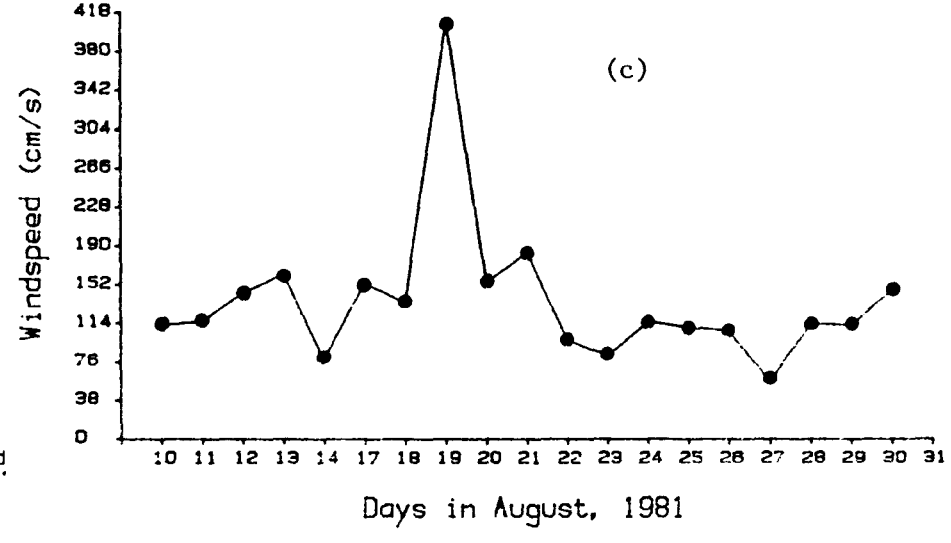
b) M. secalis

c) N. janthina

d) N. comes







N. pronuba, windspeed and temperature, August, 1981.

a) N. pronuba
b) Nightly mean temperature
c) Nightly mean windspeed

Figure 4

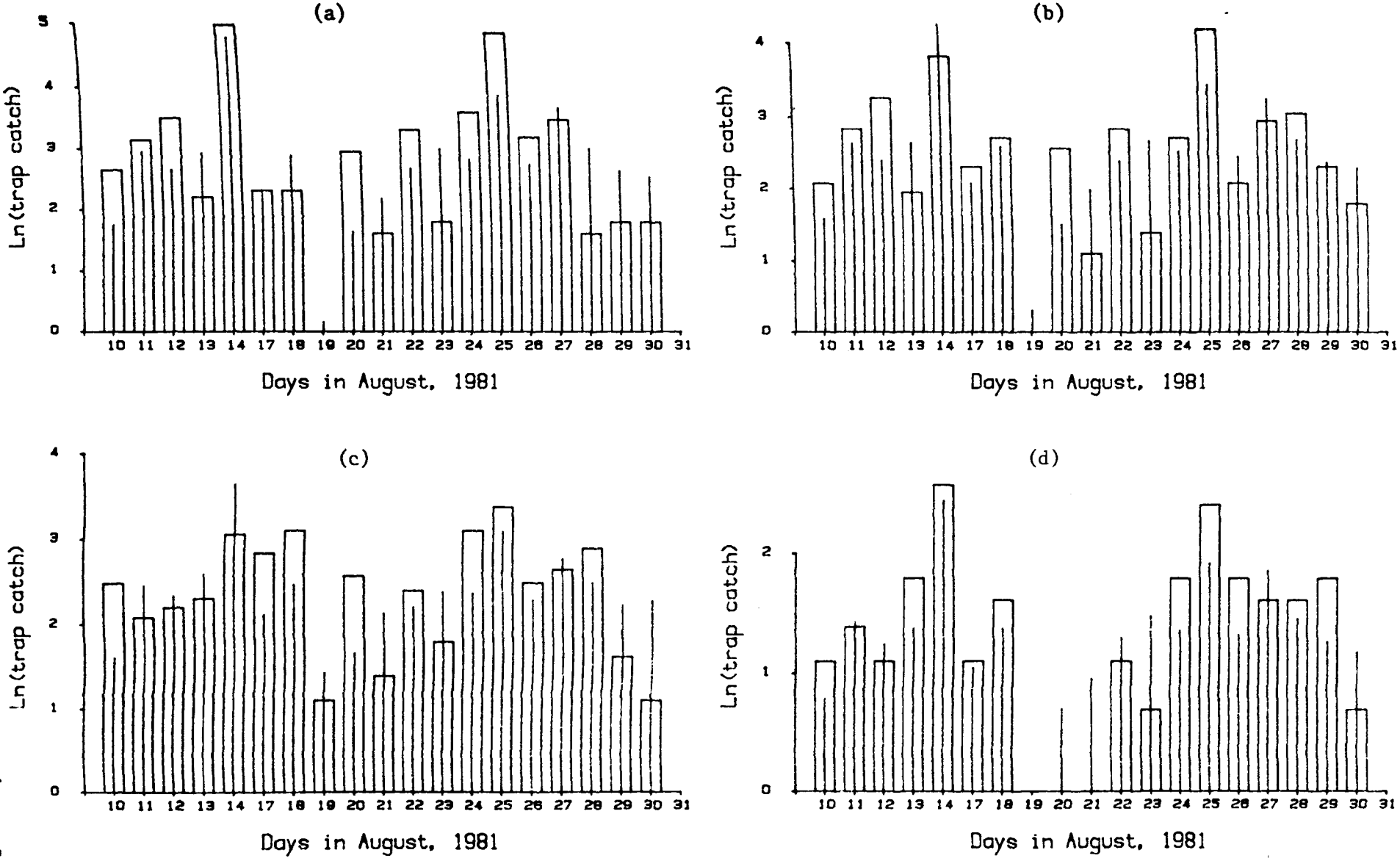


Figure 5

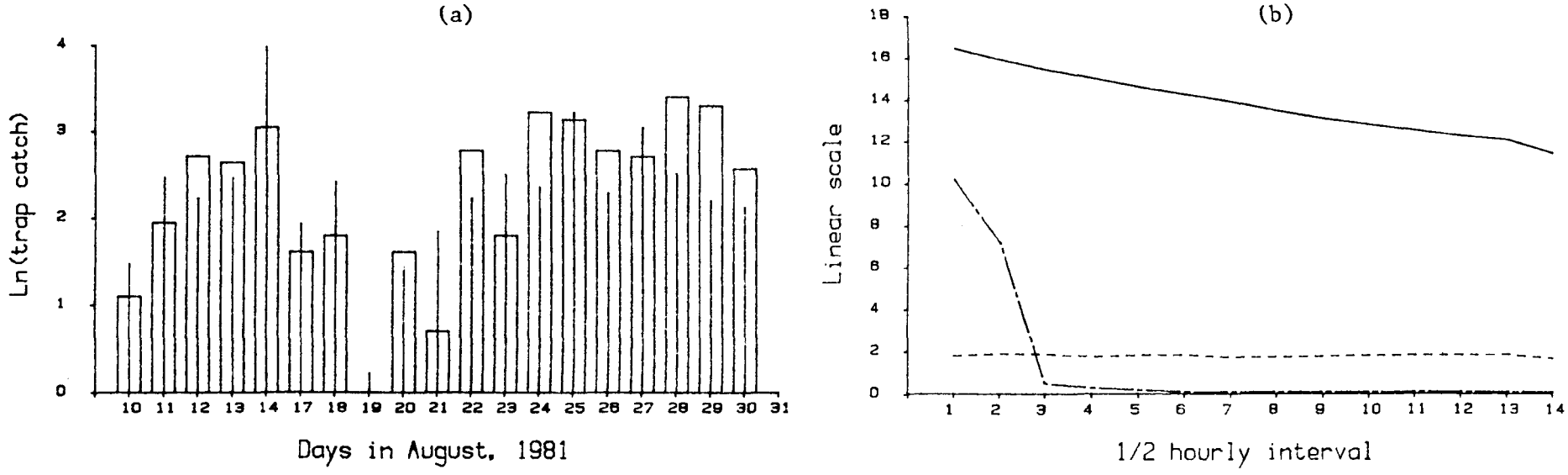
Ln (catch) overlayed with expected: (solid lines)

a) A. tristella

b) M. secalis

c) N. janthina

d) N. comes



a) Ln (catch) overlayed with expected (solid lines) N. pronuba.

b) Averaged nightly form of meteorological conditions, taken over 19 nights.
Solid line - temperature, ^{o}C.
Dashed line - windspeed, m/s.
Dot-dashed line - Lux X2
$\frac{1}{2}$ hourly intervals commence at 21.00 BST.

Figure 6

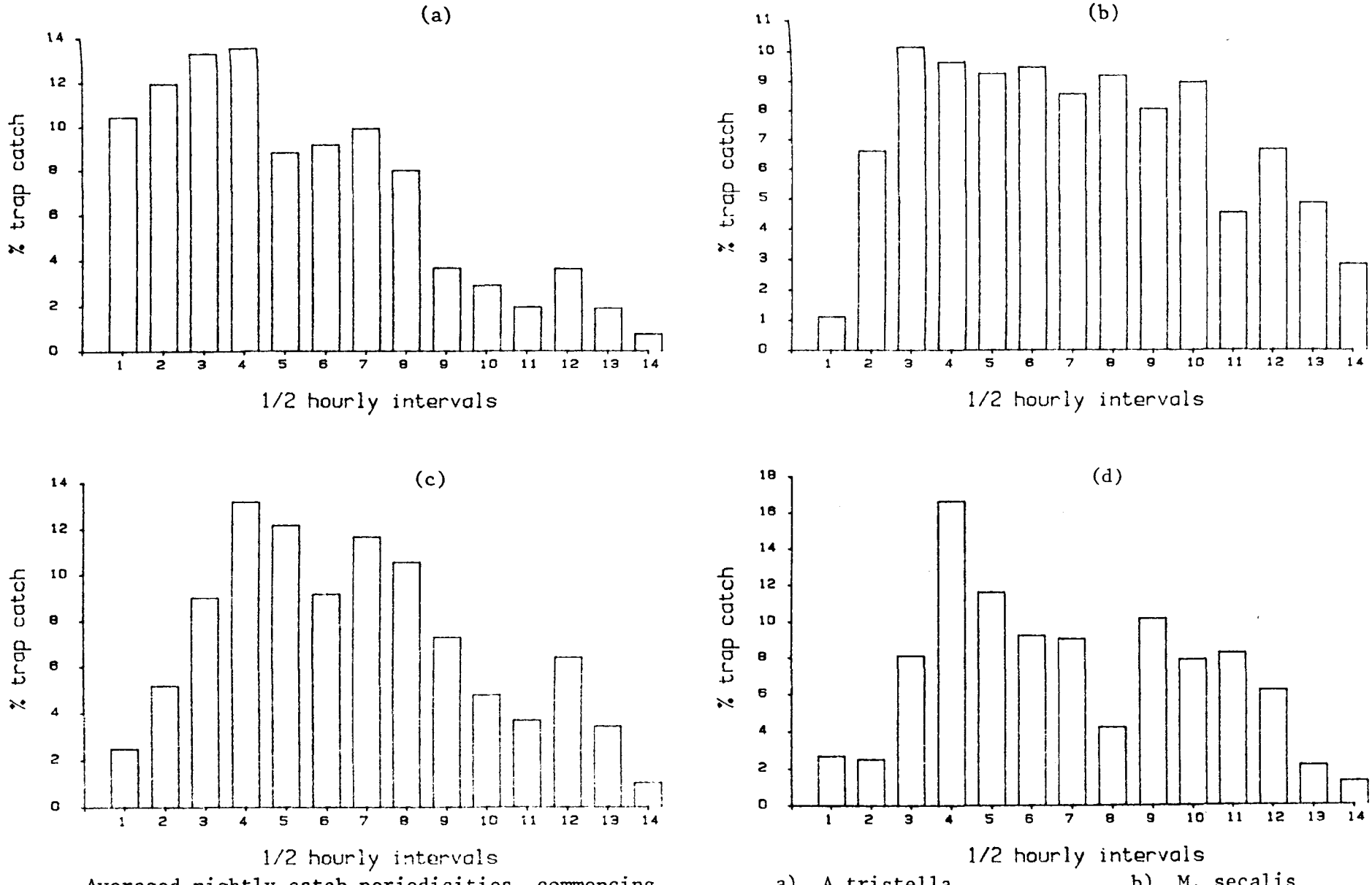
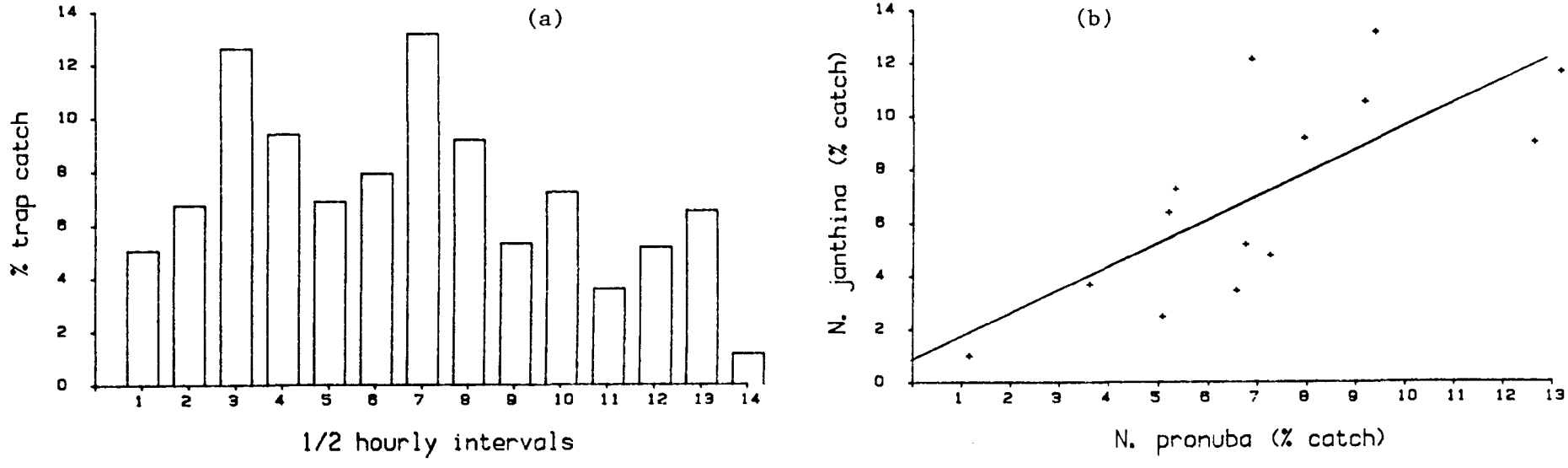


Figure 7

Averaged nightly catch periodicities, commencing at 21.00 BST.

a) A tristella b) M. secalis

c) N. janthina d) N. comes

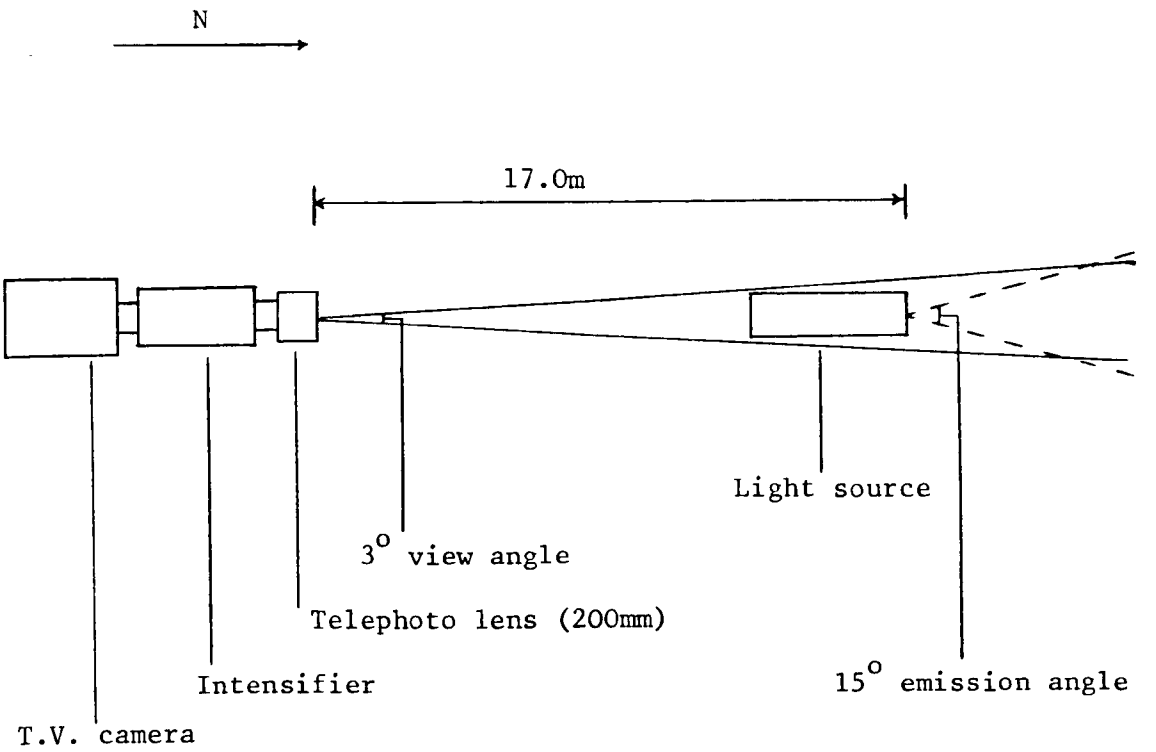


Catch periodicity comparison

a) Averaged nightly catch periodicity for N. pronuba, commencing at 21.00 BST.

b) A comparison of the catch periodicities of two species of Noctuid moths.

Figure 8



In-line Camera Plan (Top view)

Figure 9a

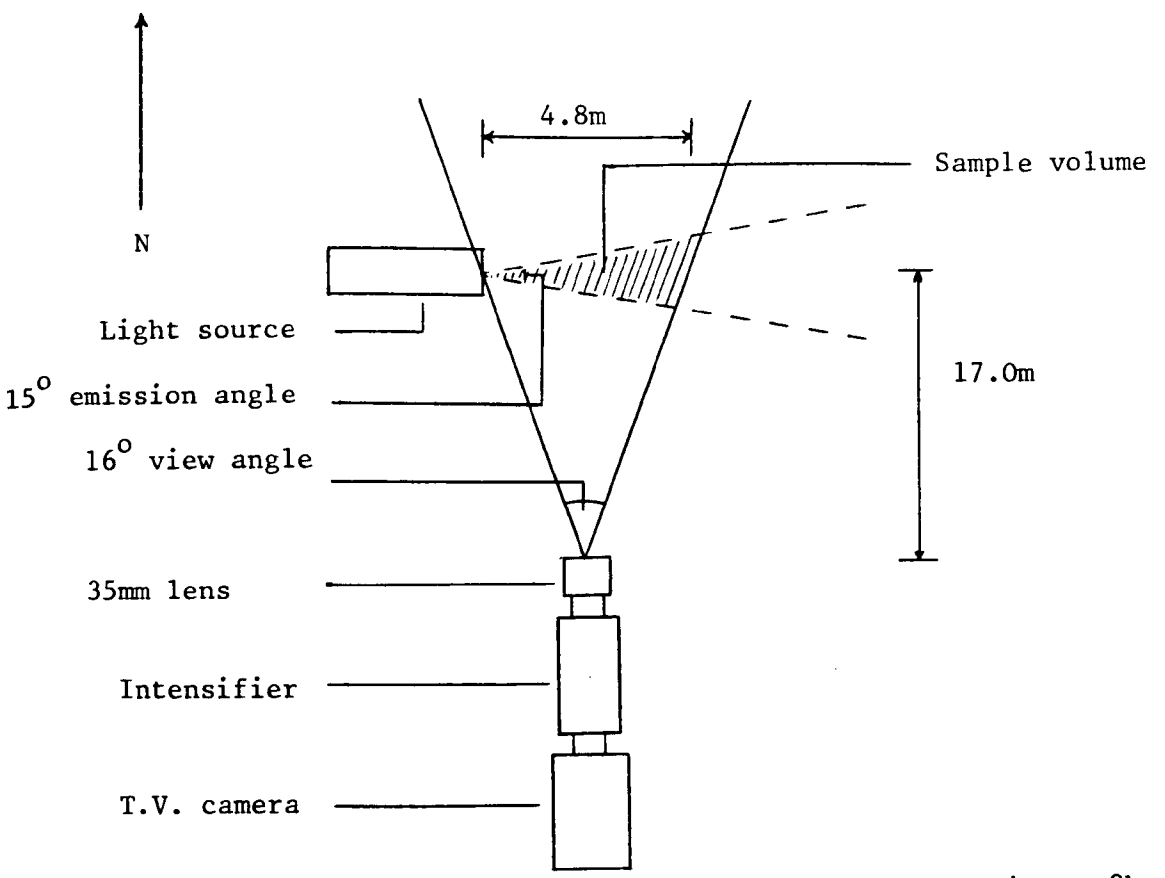


Figure 9b

Camera Plan at 90° (Top view)

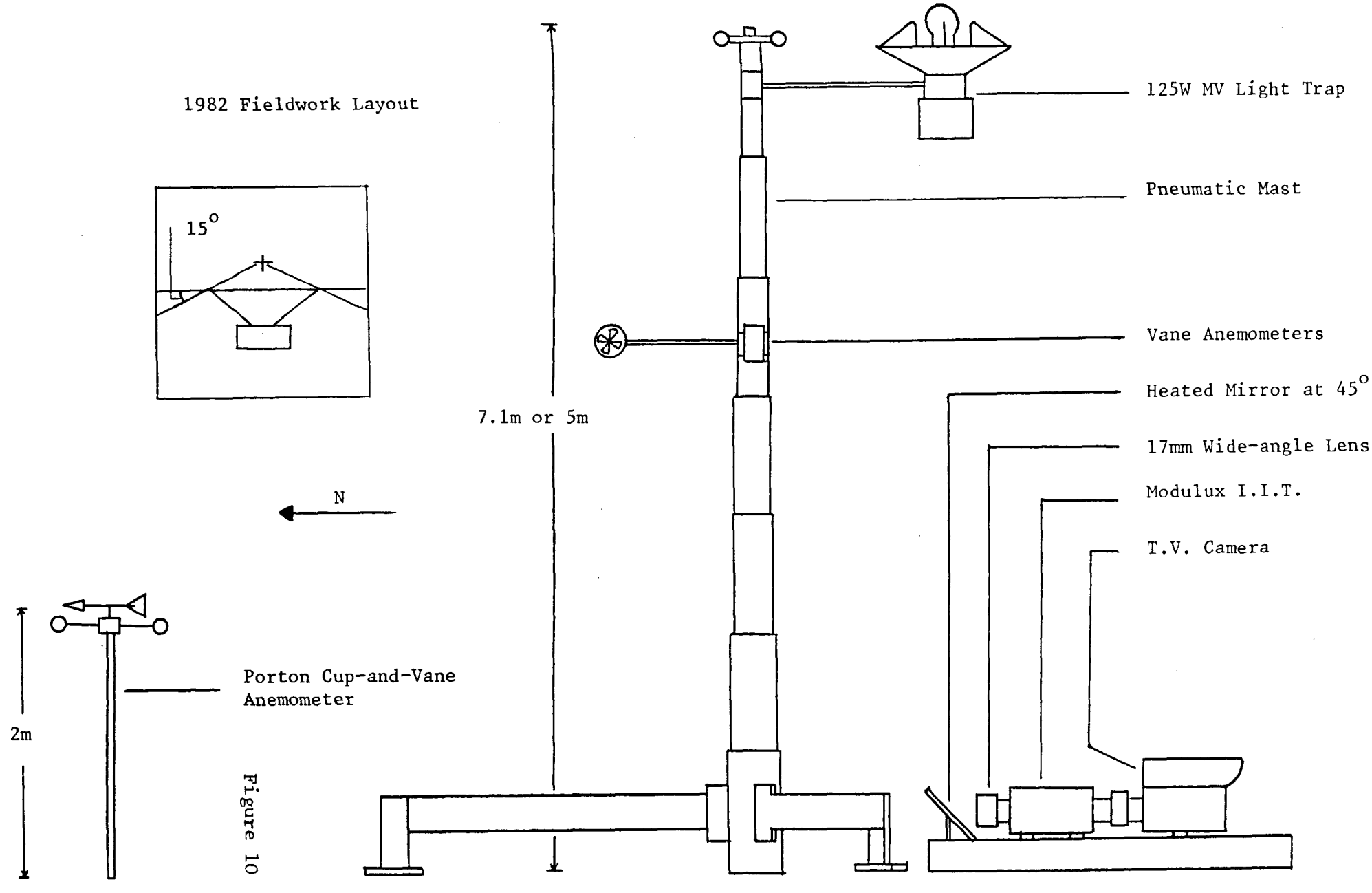
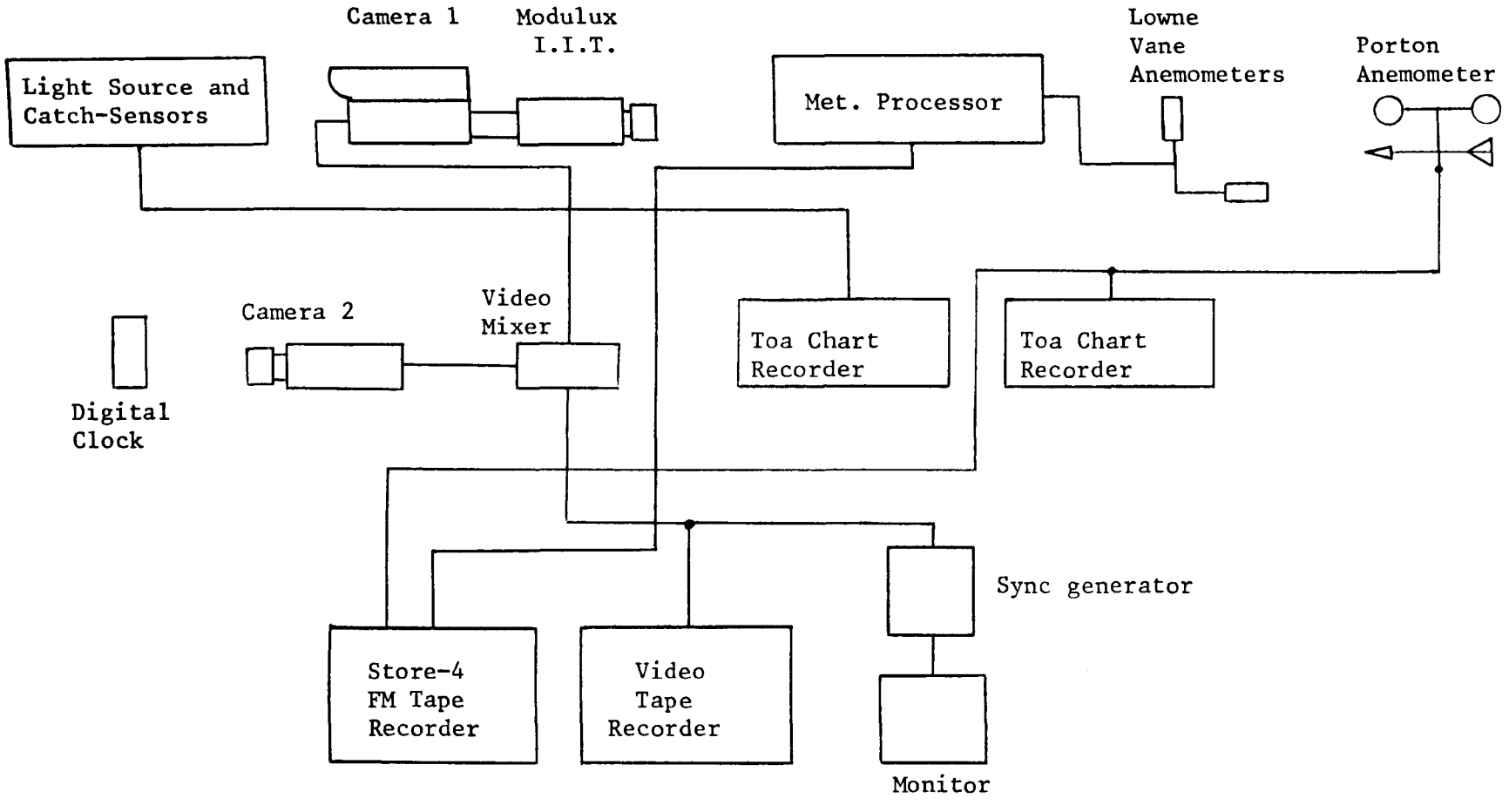

1982 Fieldwork Layout
15°
7.1m or 5m
N
125W MV Light Trap
Pneumatic Mast
Vane Anemometers
Heated Mirror at 45°
17mm Wide-angle Lens
Modulux I.I.T.
T.V. Camera
2m
Porton Cup-and-Vane Anemometer

Figure 10



1982 Fieldwork Data Collection System

Figure 11

TIME: 4:17
GROUND VECTORS AS FOLLOWS:

	DISTANCE	GRID-REF	COURSE	APPROACH	N/S WIND VECTOR	E/W WIND VECTOR	RES. WIND SPEED	RES. WIND DIRECTION	ELAPSED TIME
MEAN SPEED: 2.296									
MIN SPEED: .8474	1.193	10 ,8	33.69	NEG	1.107	.8636	1.404	217.9	1.1
MAX SPEED: 4.237	2.093	11 ,9	56.30	NEG	1.107	.8636	1.404	217.9	1.5
MAX ACCEL: 13.06	1.720	11 ,8	74.05	NEG	1.107	.8636	1.404	217.9	1.4
MAX DECCL: -13.5	1.134	10 ,8	18.43	NEG	1.107	.8636	1.404	217.9	1
MAX AN.VL: 6.716	1.193	10 ,8	78.69	NEG	1.107	.8636	1.404	217.9	1.1

FLIGHT PATH:

RADIUS (M.)	TIME SECS.	(%)	GRID-REF	TIME SECS.	(%)
0.0 - .25	0	0	10 ,8	.4	26.66
.25 - 0.5	0	0	9 ,6	.3	20
0.5 - .75	0	0	8 ,5	.2	13.33
.75 - 1.0	.5	33.33	8 ,3	.1	6.666
1.0 -1.25	.5	33.33	8 ,4	.1	6.666
1.25- 1.5	.3	20	9 ,7	.1	6.666
1.5 -1.75	.1	6.666	10 ,7	.1	6.666
1.75- 2.0	0	0	11 ,8	.1	6.666
2.0 -2.25	.1	6.666	11 ,9	.1	6.666
2.25- 2.5	0	0	0 ,0	0	0
2.5 -2.75	0	0	0 ,0	0	0
RAD>=2.75	0	0	0 ,0	0	0

TIME	SPEED	DISTANCE
.1	3.196	1.489
.2	3.854	1.233
.3	2.945	1.030
.4	1.835	.9168
.5	1.051	.9415
.6	.9971	.9755
.7	1.789	.9603
.8	2.627	.9799
.9	2.839	1.057
1	1.486	1.134
1.1	.8474	1.193
1.2	1.198	1.272
1.3	2.115	1.445
1.4	3.422	1.720
1.5	4.237	2.093

TIME: 4:17
AIR VECTORS AS FOLLOWS:

	DISTANCE	GRID-REF	COURSE	APPROACH	N/S WIND VECTOR	E/W WIND VECTOR	RES. WIND SPEED	RES. WIND DIRECTION	ELAPSED TIME
MEAN SPEED: 1.372									
MIN SPEED: .4967	.8917	8 ,5	307.6	POS	1.107	.8636	1.404	217.9	1
MAX SPEED: 2.938	1.281	9 ,5	64.96	NEG	1.107	.8636	1.404	217.9	1.5
MAX ACCEL: 10.04	1.195	8 ,4	93.57	NEG	1.107	.8636	1.404	217.9	1.4
MAX DECCL: -10.2	1.149	8 ,4	82.88	000	1.107	.8636	1.404	217.9	.4
MAX AN.VL: 22.30	1.239	8 ,4	348.5	POS	.8636	.8636	1.221	225.0	.6

Sample output from the programme FLITRAP, corresponding to the trajectory shown overleaf (Figure 13)

Figure 12

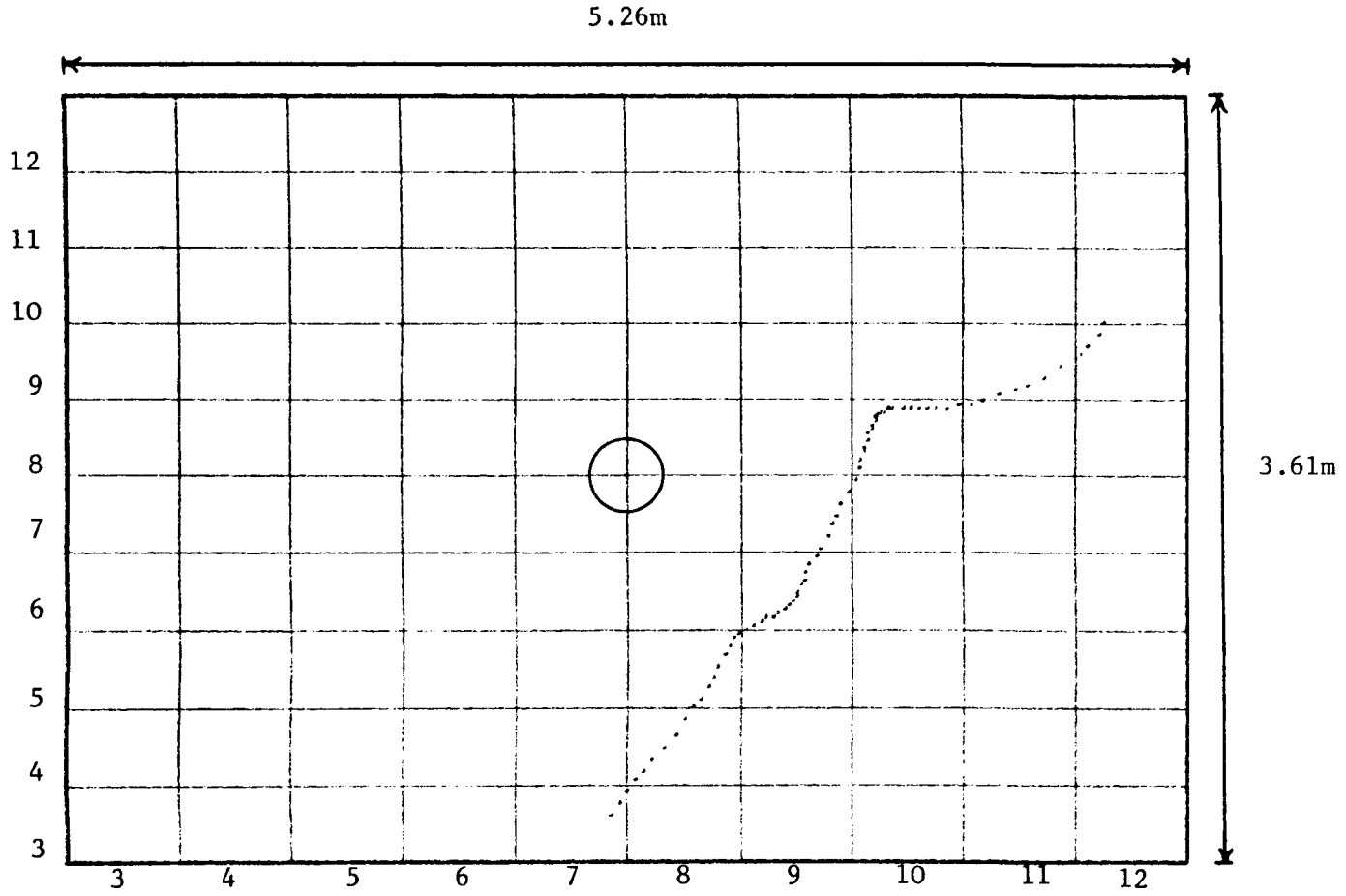


Figure 13

Moth-track with grid overlay
(See previous Figure for track statistics).

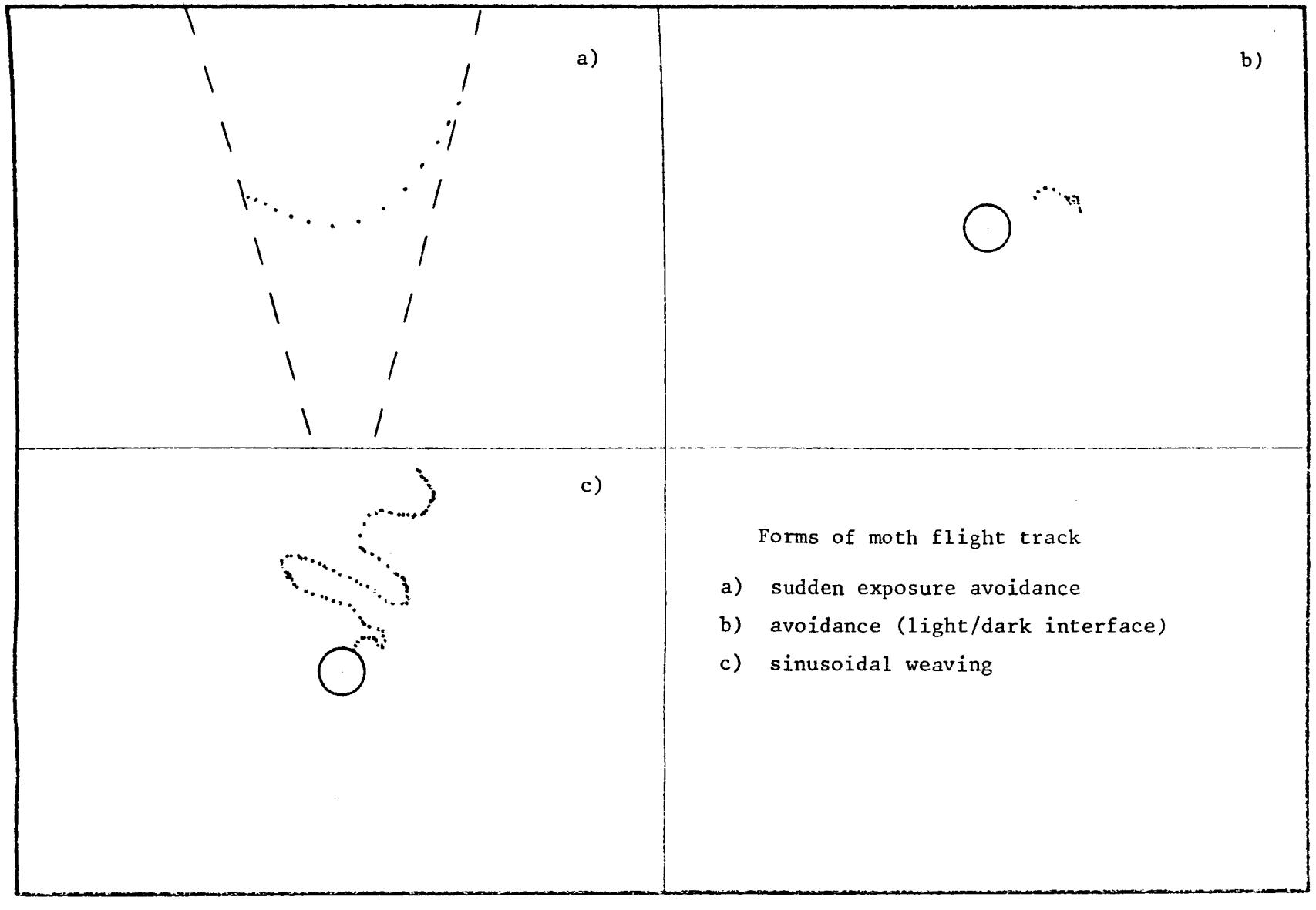
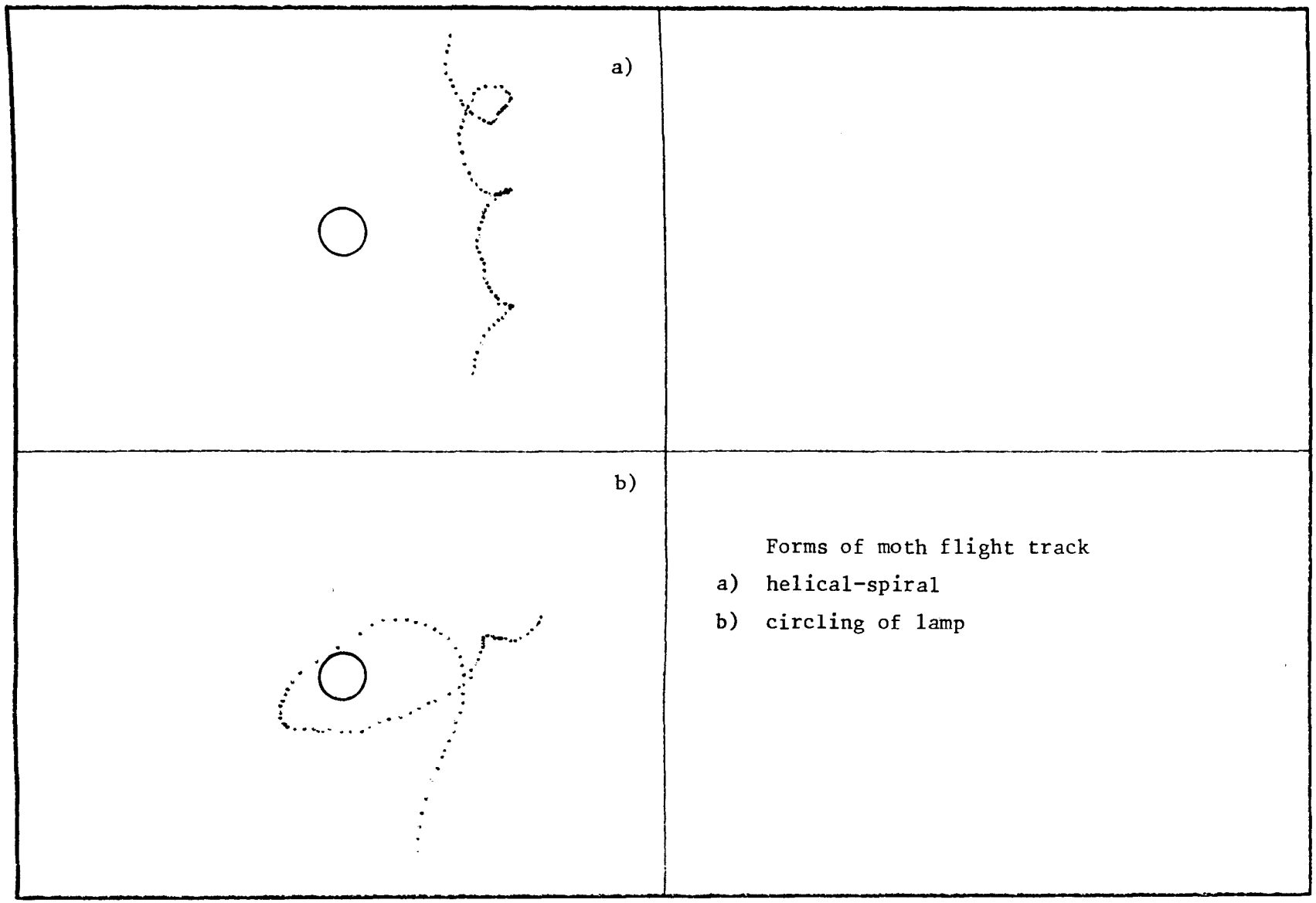

a)
b)
c)
Forms of moth flight track
a) sudden exposure avoidance
b) avoidance (light/dark interface)
c) sinusoidal weaving

Figure 14

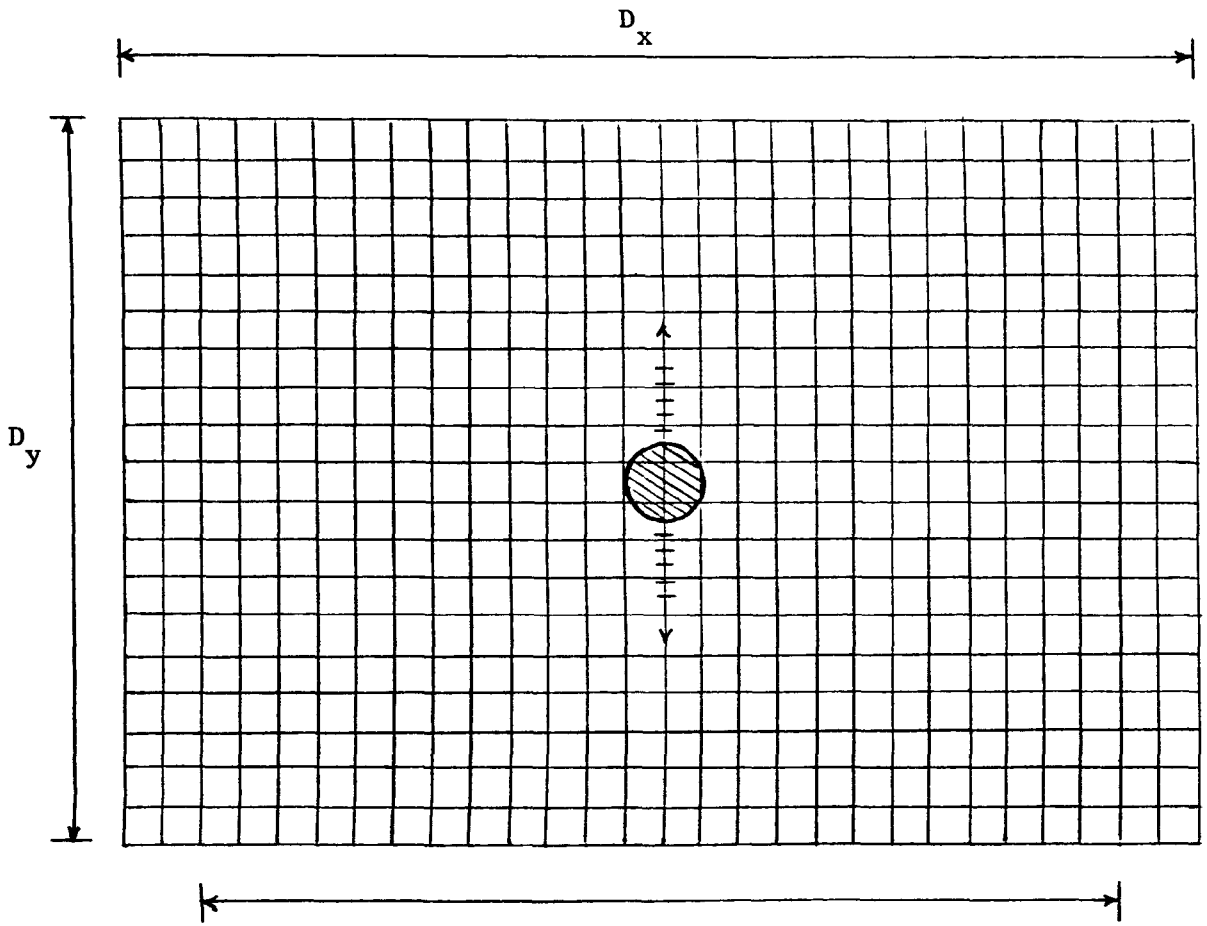


Forms of moth flight track

a) helical-spiral

b) circling of lamp

Figure 15



D_x is 3.81m or 5.26m (trap at 5m or 7.1m).

D_y is 2.62m or 3.61m.

Short vertical ticks indicate relative thickness of annuli (5cm), used in estimating radial densities.

Shaded circle denotes trap position (size relative to height of 5m).

Figure 16

Dimensions of screen visual area

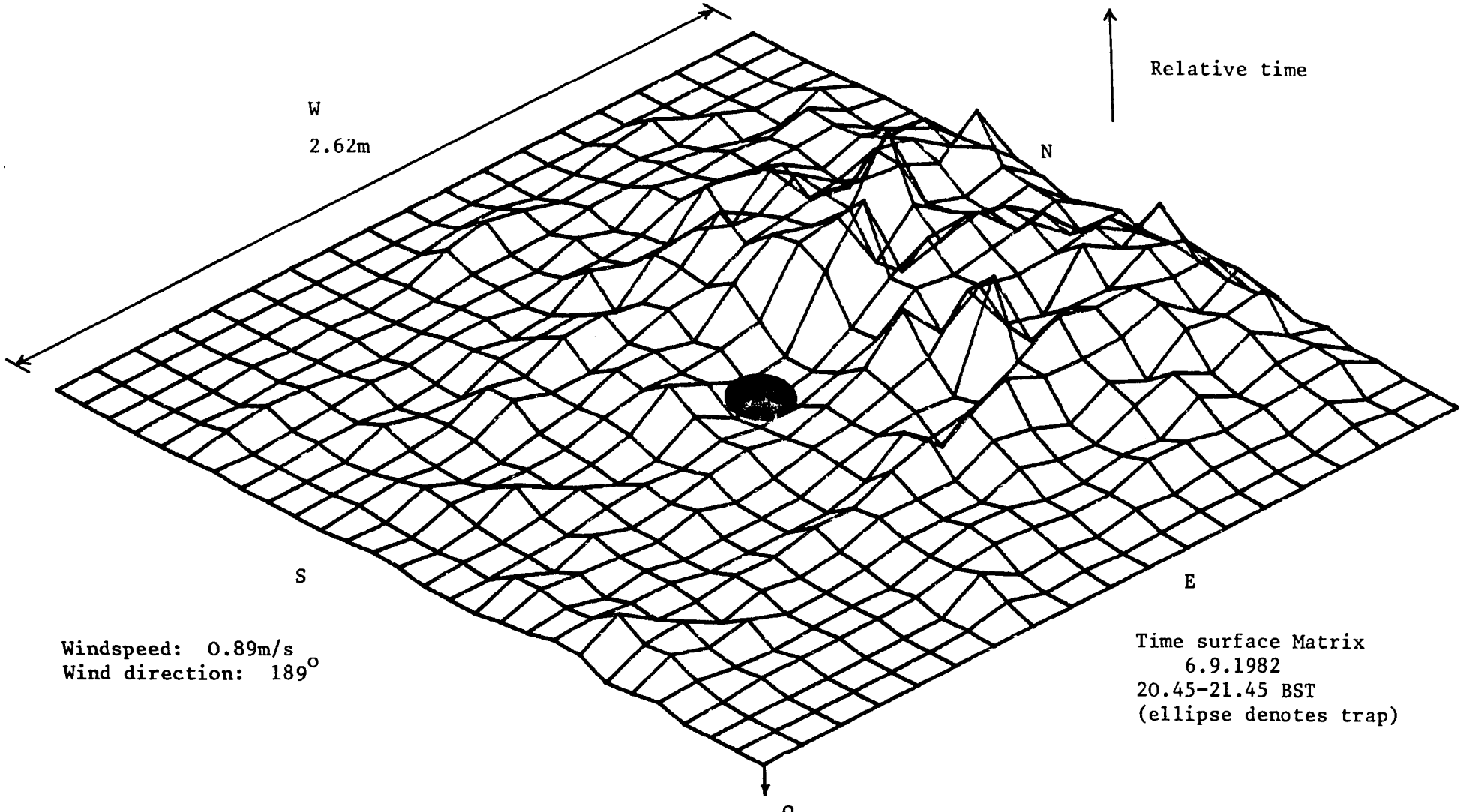
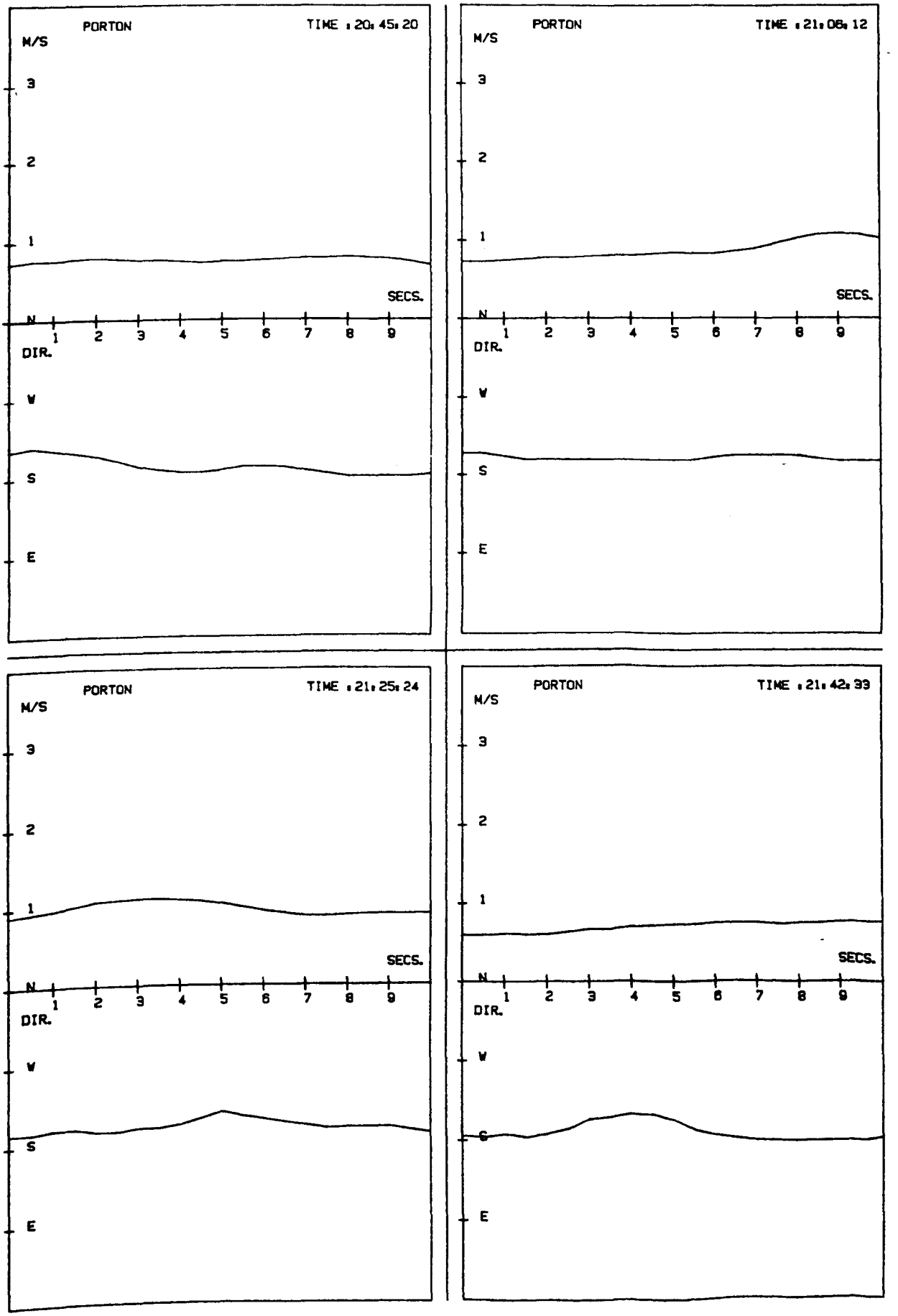
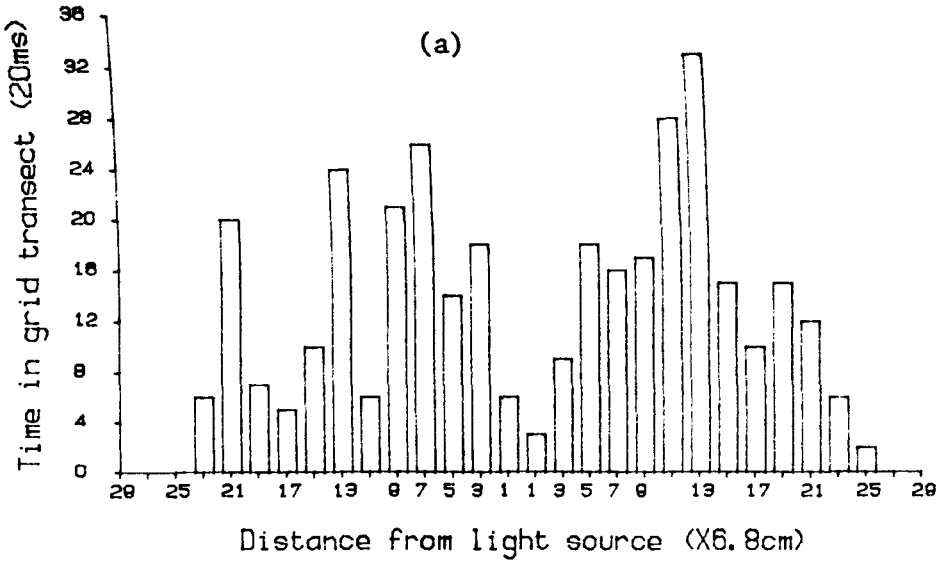

W
2.62m
N
Relative time
S
E
Windspeed: 0.89m/s
Wind direction: 189°
Time surface Matrix
6.9.1982
20.45-21.45 BST
(ellipse denotes trap)
135°
(compass bearing)

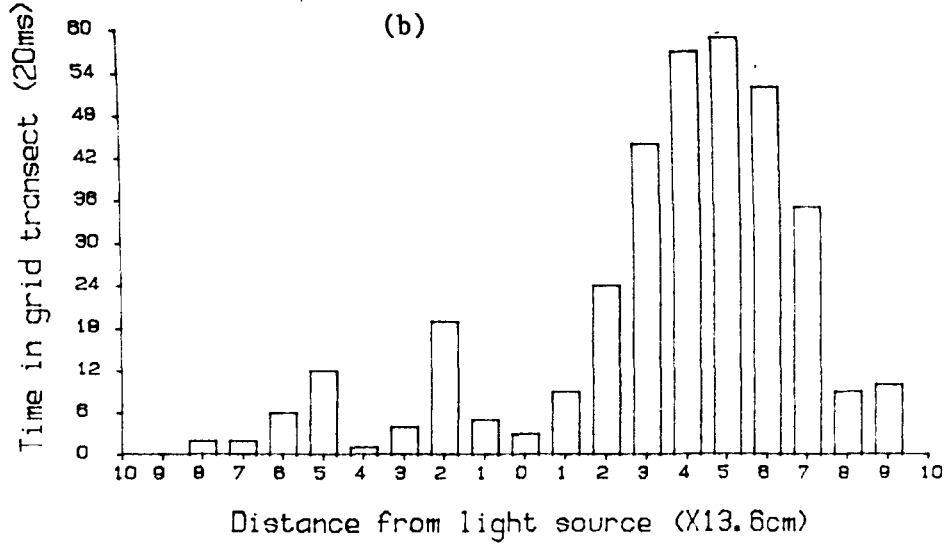
Figure 17

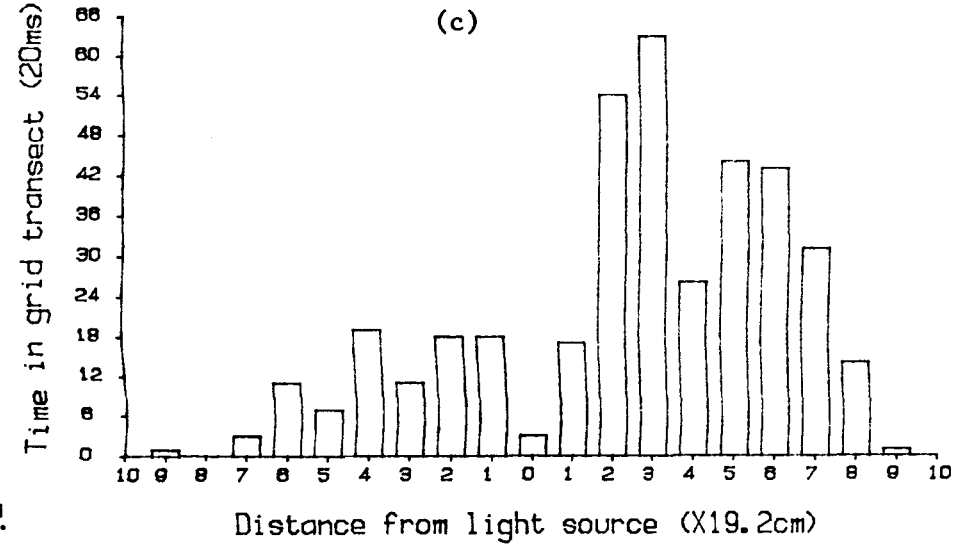


Wind-trace samples, 6/9/1982

Figure 18







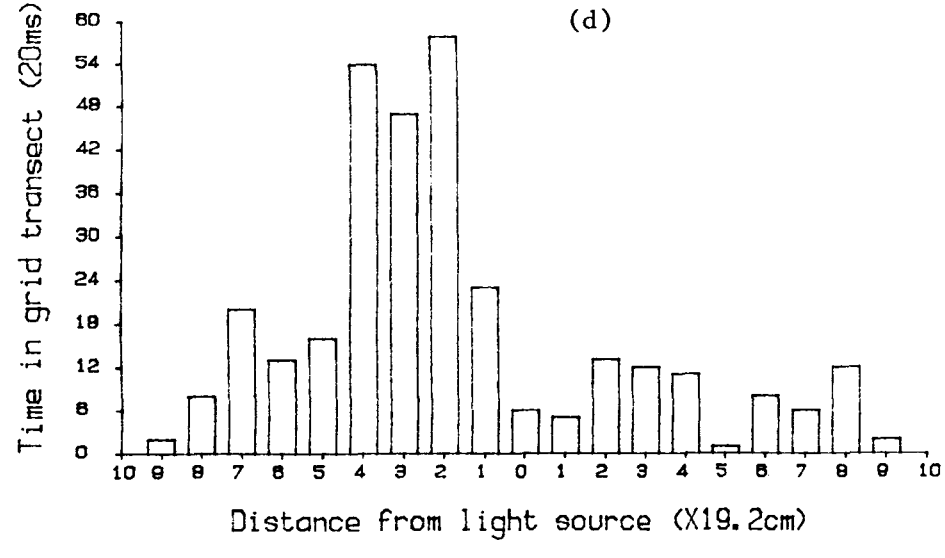


Figure 19

Transects across TSM, 6.9.1982.

a) W/E
b) S/N
c) SW/NE
d) NW/SE

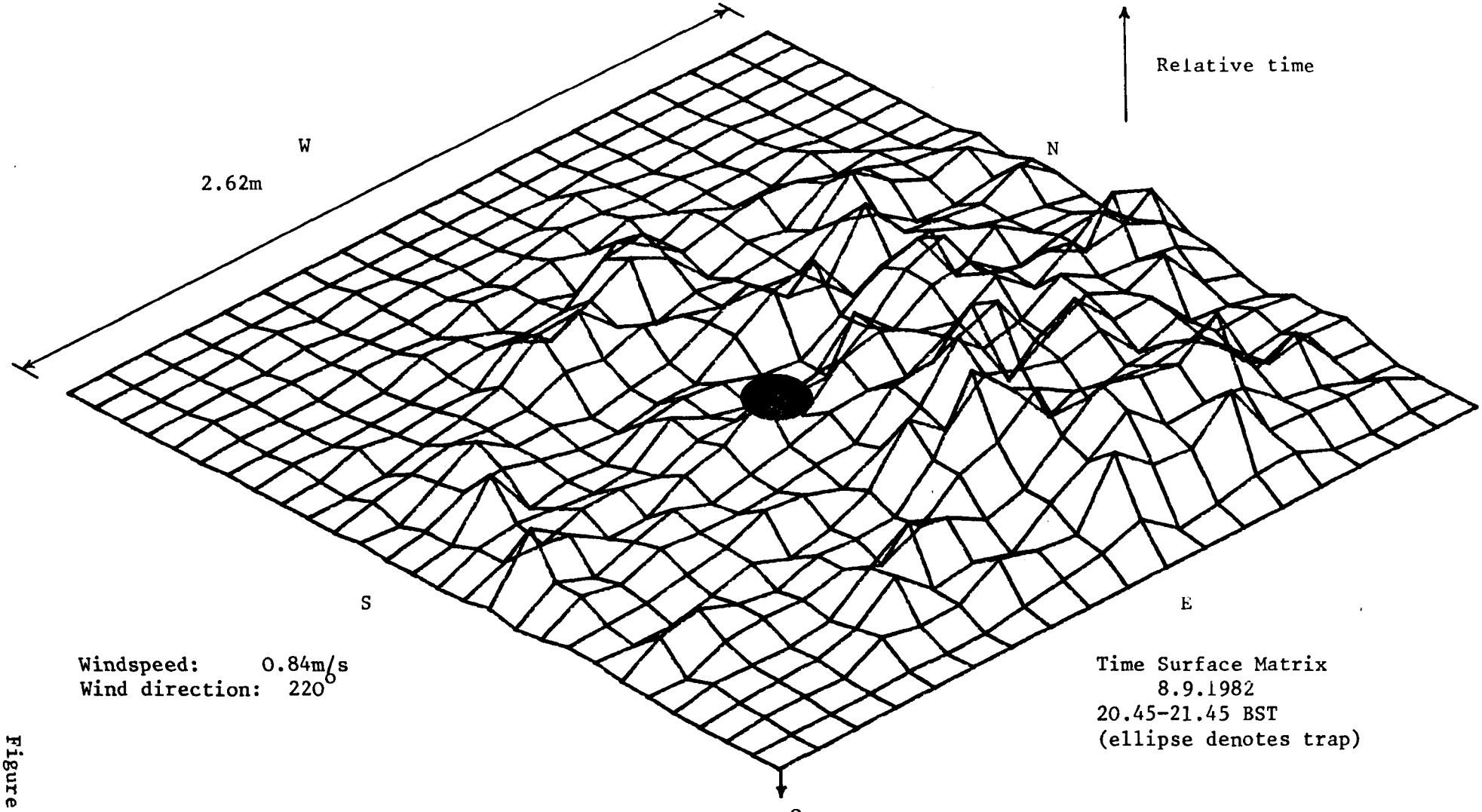
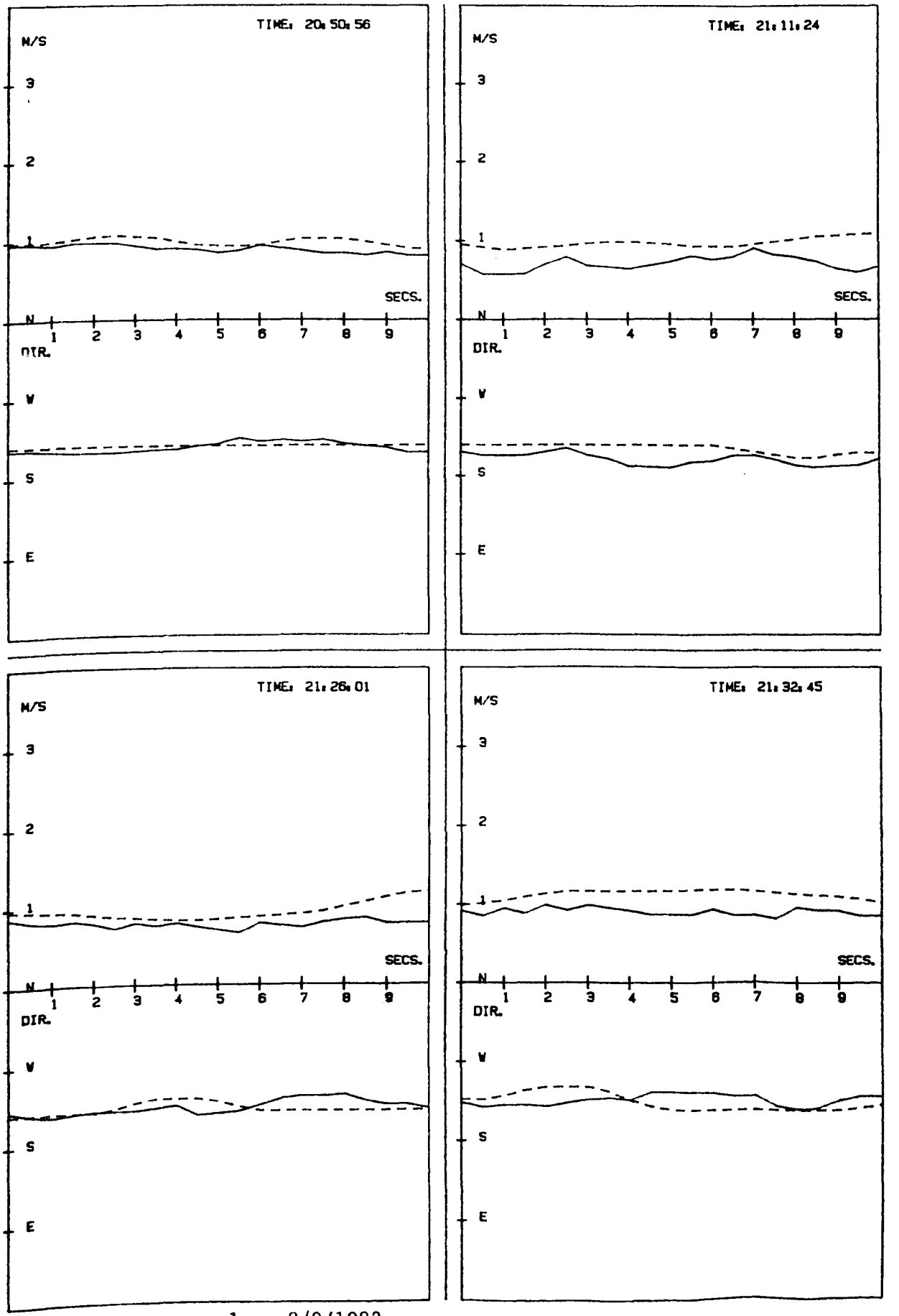
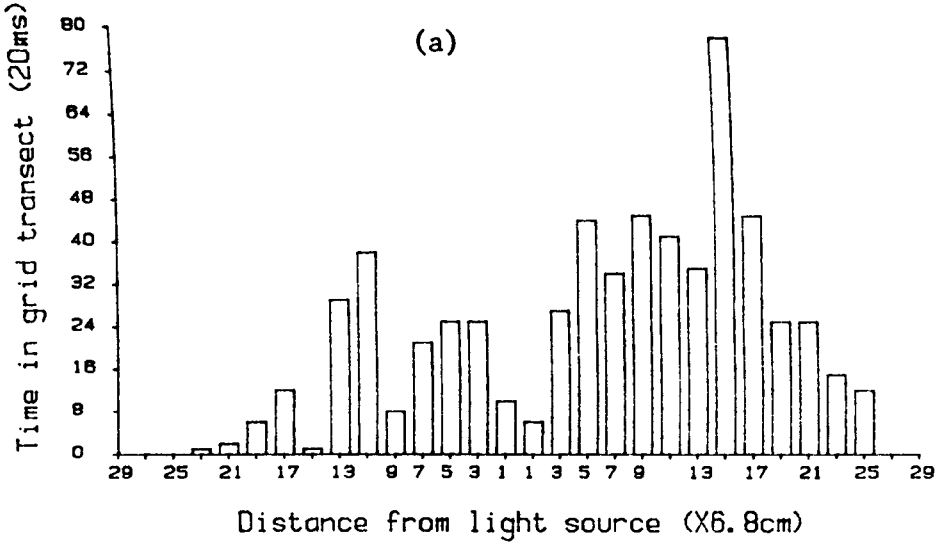

Relative time
W
2.62m
N
S
E
Windspeed: 0.84m/s
Wind direction: 220°
Time Surface Matrix
8.9.1982
20.45-21.45 BST
(ellipse denotes trap)
135°
(compass bearing)

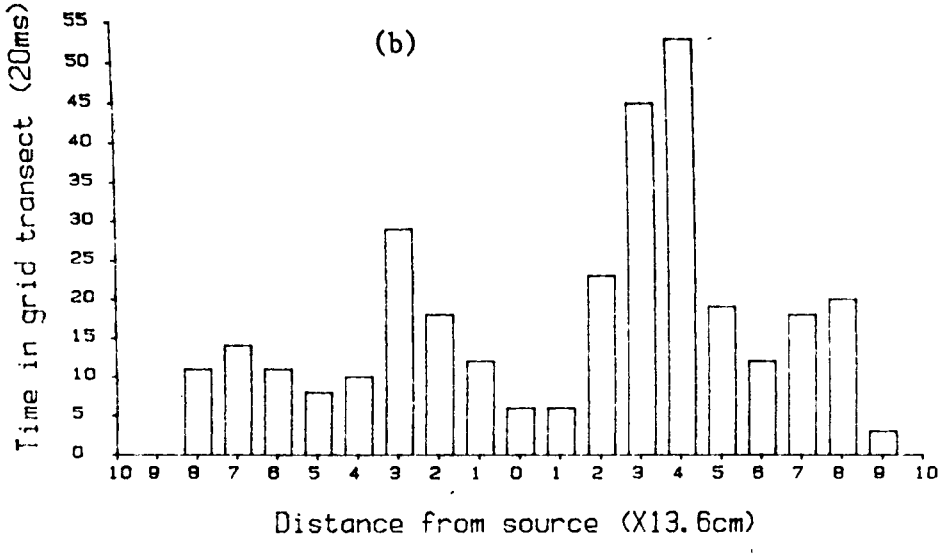
Figure 20

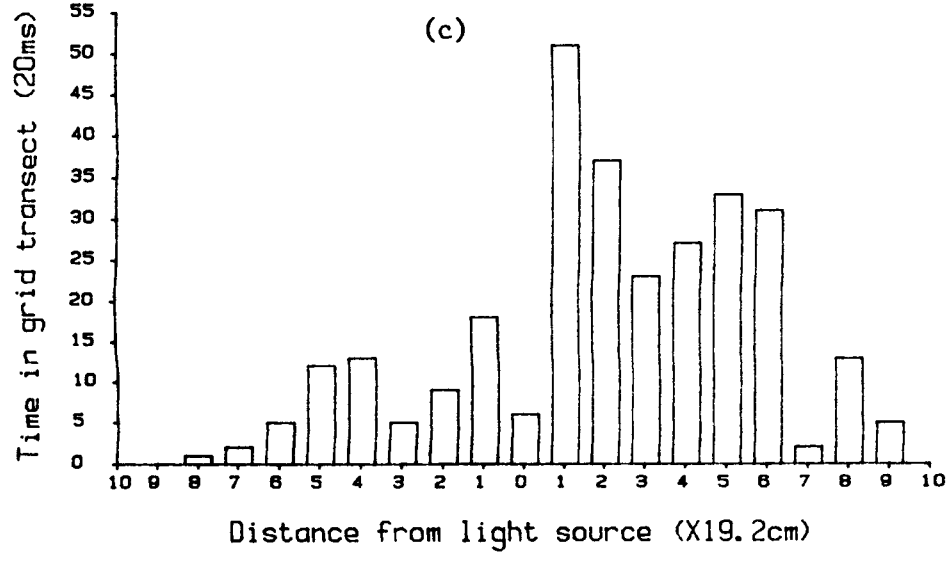


Wind-trace samples, 8/9/1982.
Solid lines - Lowne vanes
Dashed lines - Porton

Figure 21







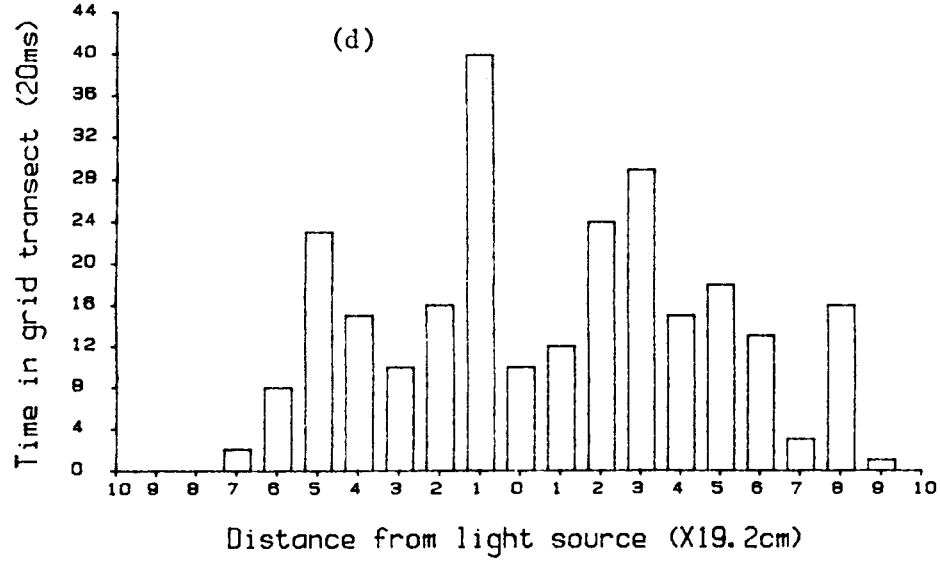


Figure 22

Transects across TSM, 8.9.1982

a) W/E b) S/N
c) SW/NE d) NW/SE

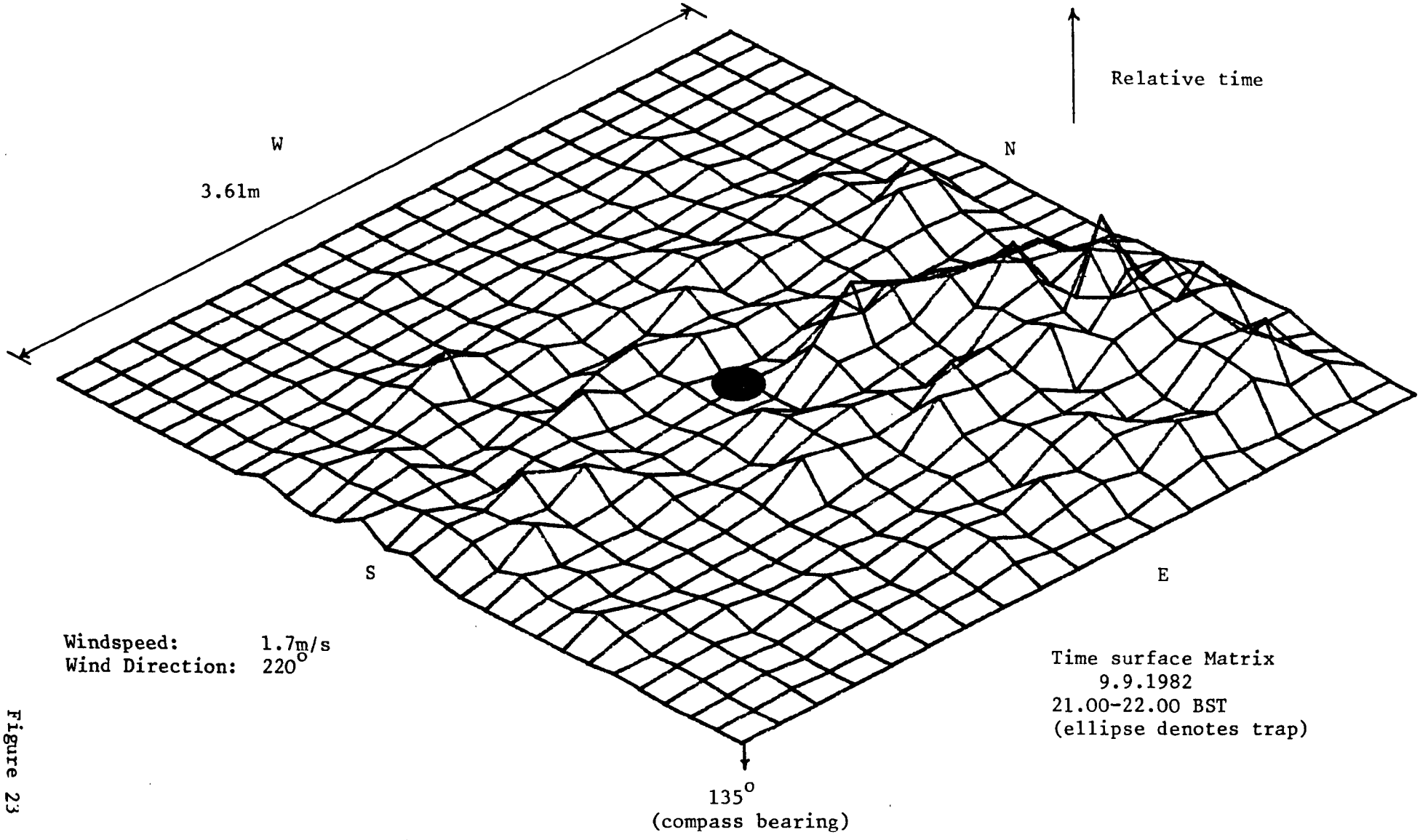
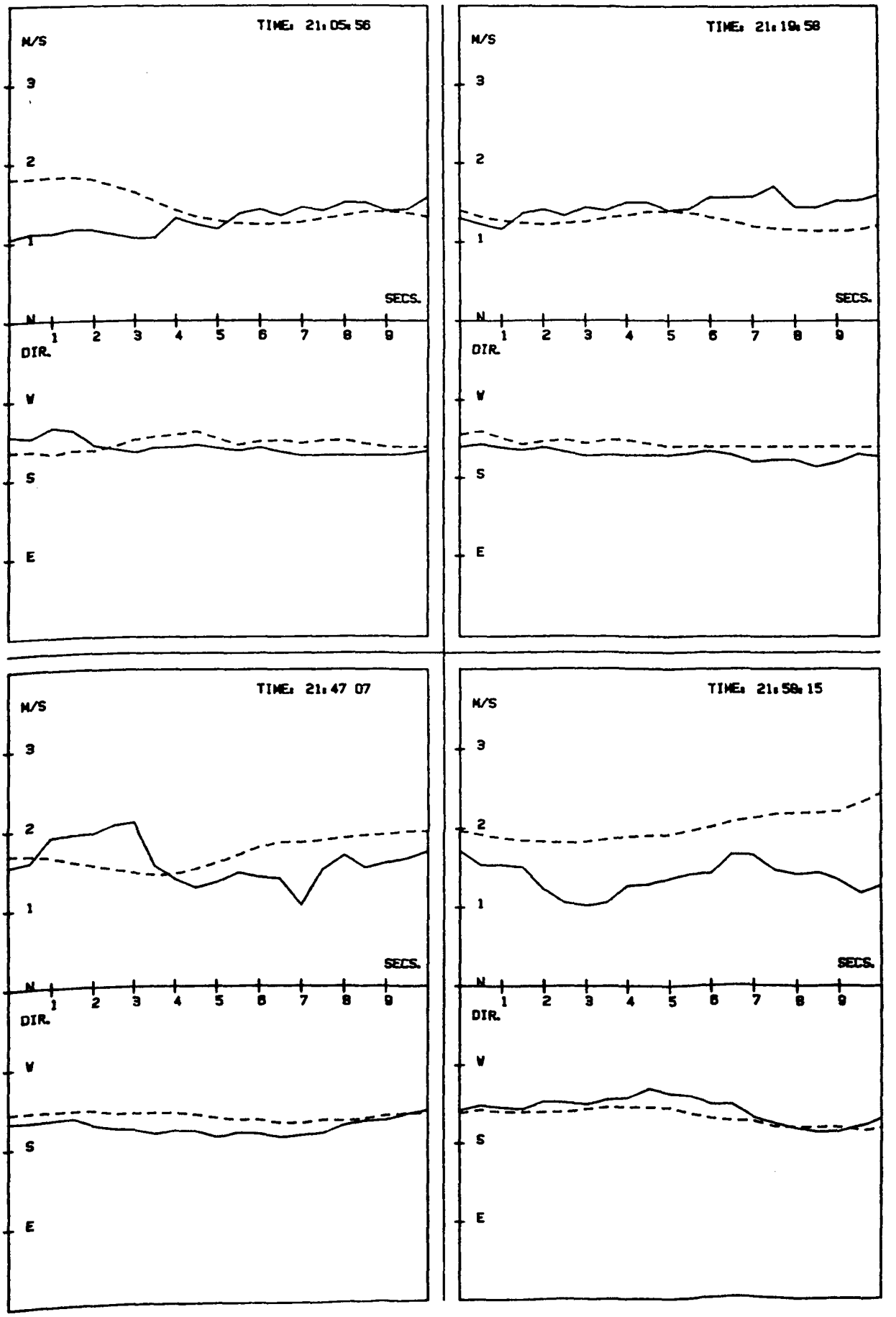

Relative time
W
3.61m
N
S
E
Windspeed: 1.7m/s
Wind Direction: 220°
Time surface Matrix
9.9.1982
21.00-22.00 BST
(ellipse denotes trap)
135°
(compass bearing)

Figure 23



Wind-trace samples, 9/9/1982
Solid lines - Lowne vanes
Dashed lines - Porton

Figure 24

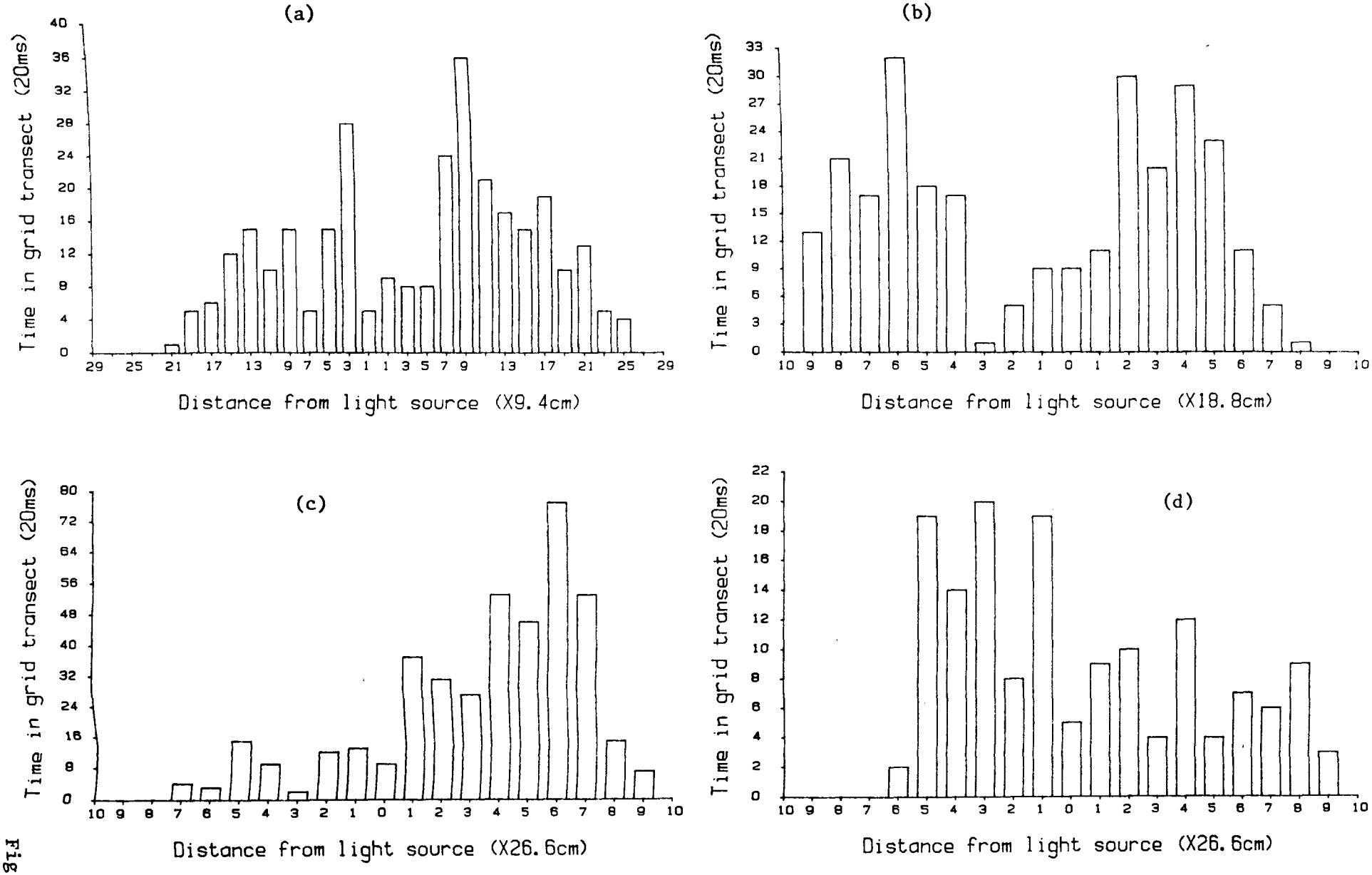


Figure 25

Transects across TSM, 9.9.1982.

a) W/E
b) S/N
c) SW/NE
d) NW/SE

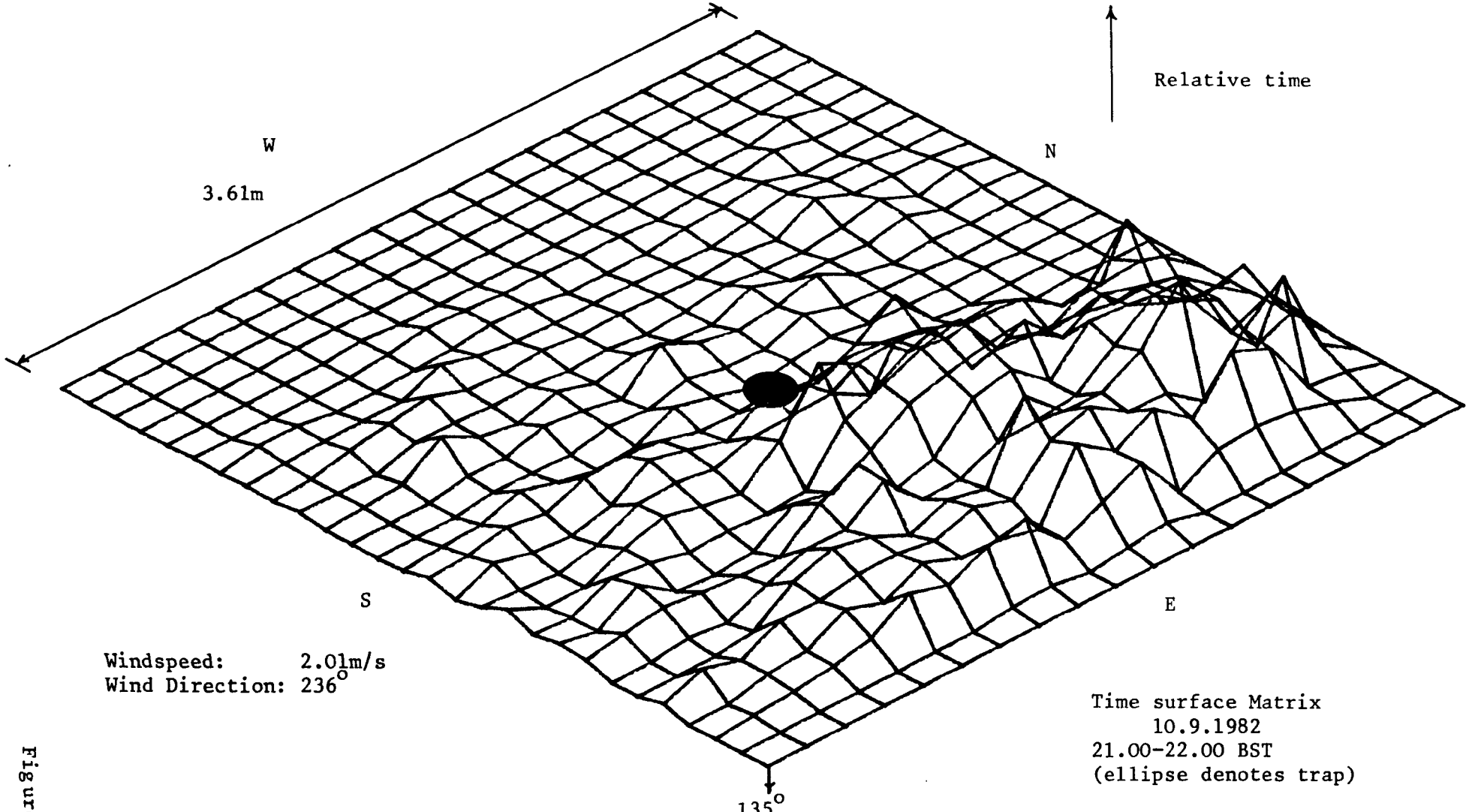
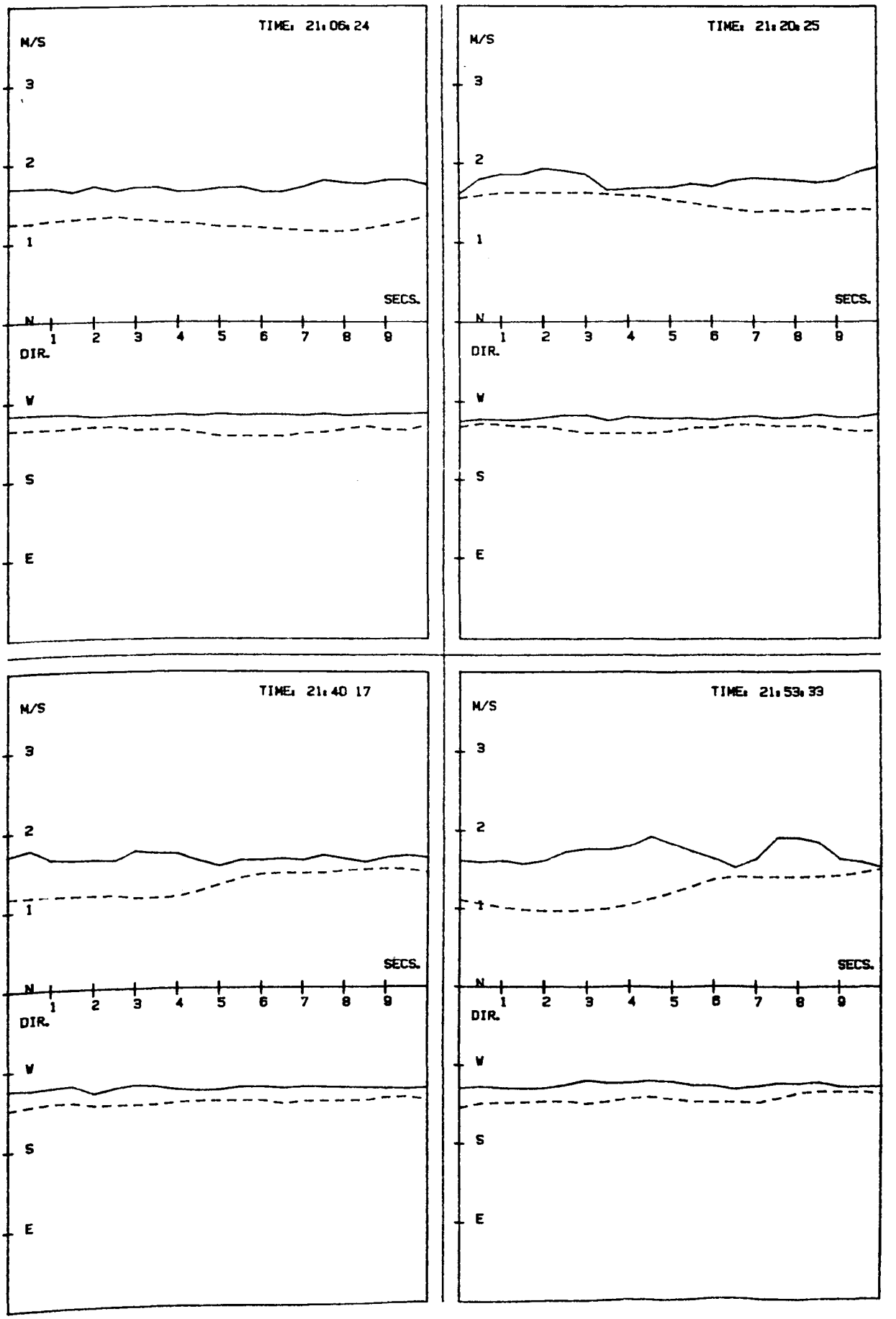

Relative time
W
3.61m
N
S
E
Windspeed: 2.01m/s
Wind Direction: 236°
Time surface Matrix
10.9.1982
21.00-22.00 BST
(ellipse denotes trap)
135°
(compass bearing)

Figure 26



Wind-trace samples, 10/9/1982

Solid lines - Lowne vanes. Dashed lines - Porton.

Figure 27

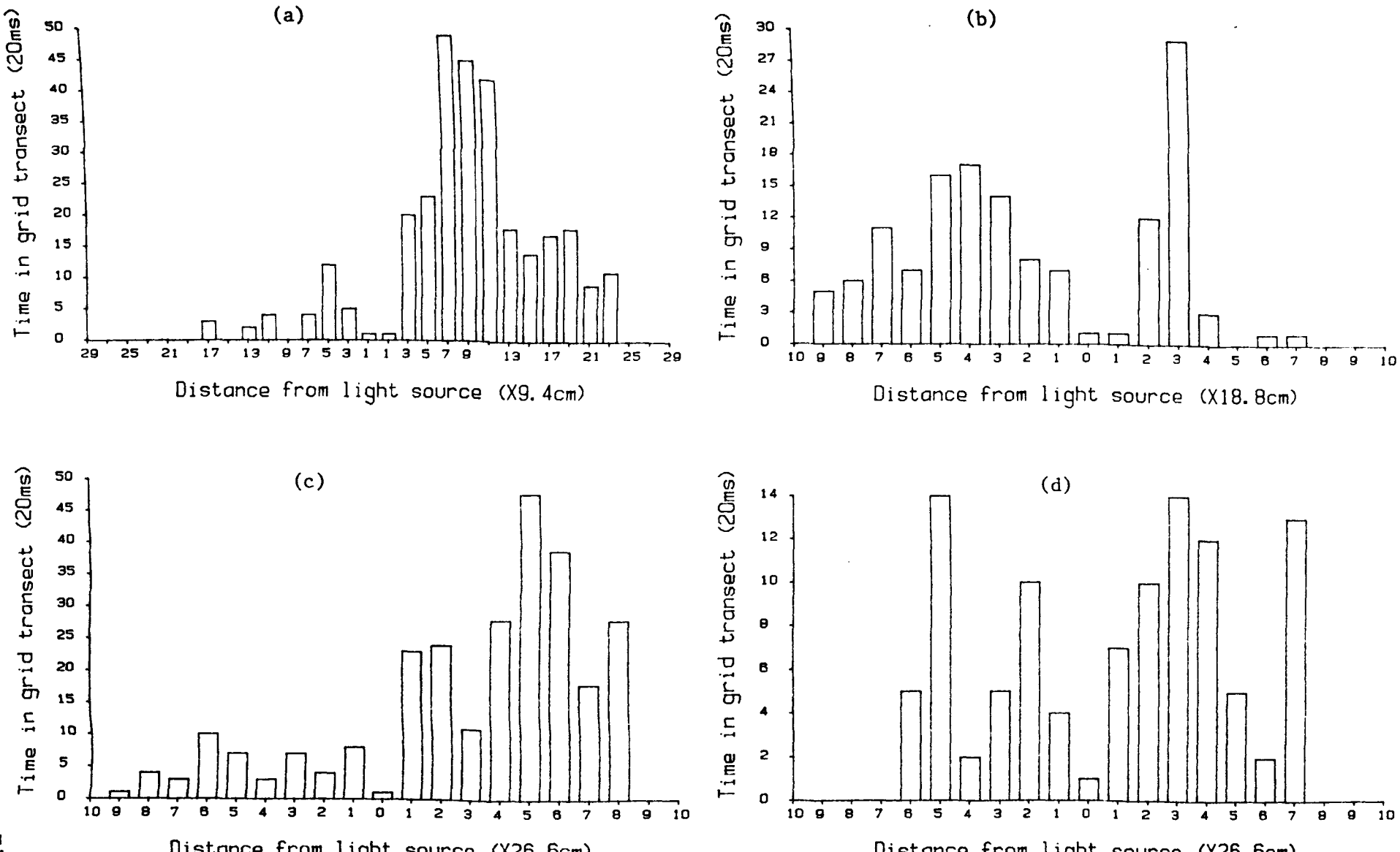


Figure 28

Transects across TSM, 10.9.1982.

a) W/E b) S/N
c) SW/NE d) NW/SE

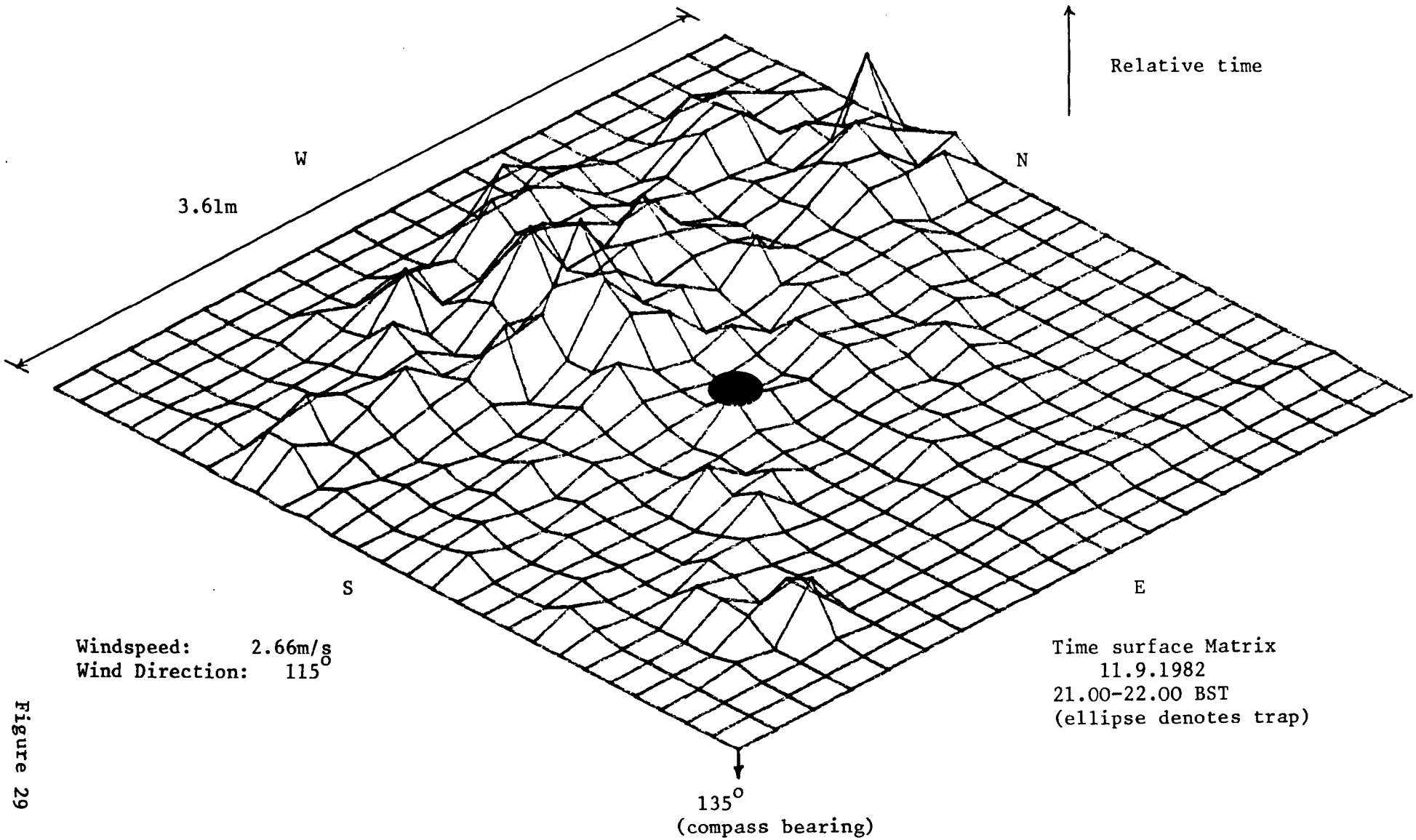
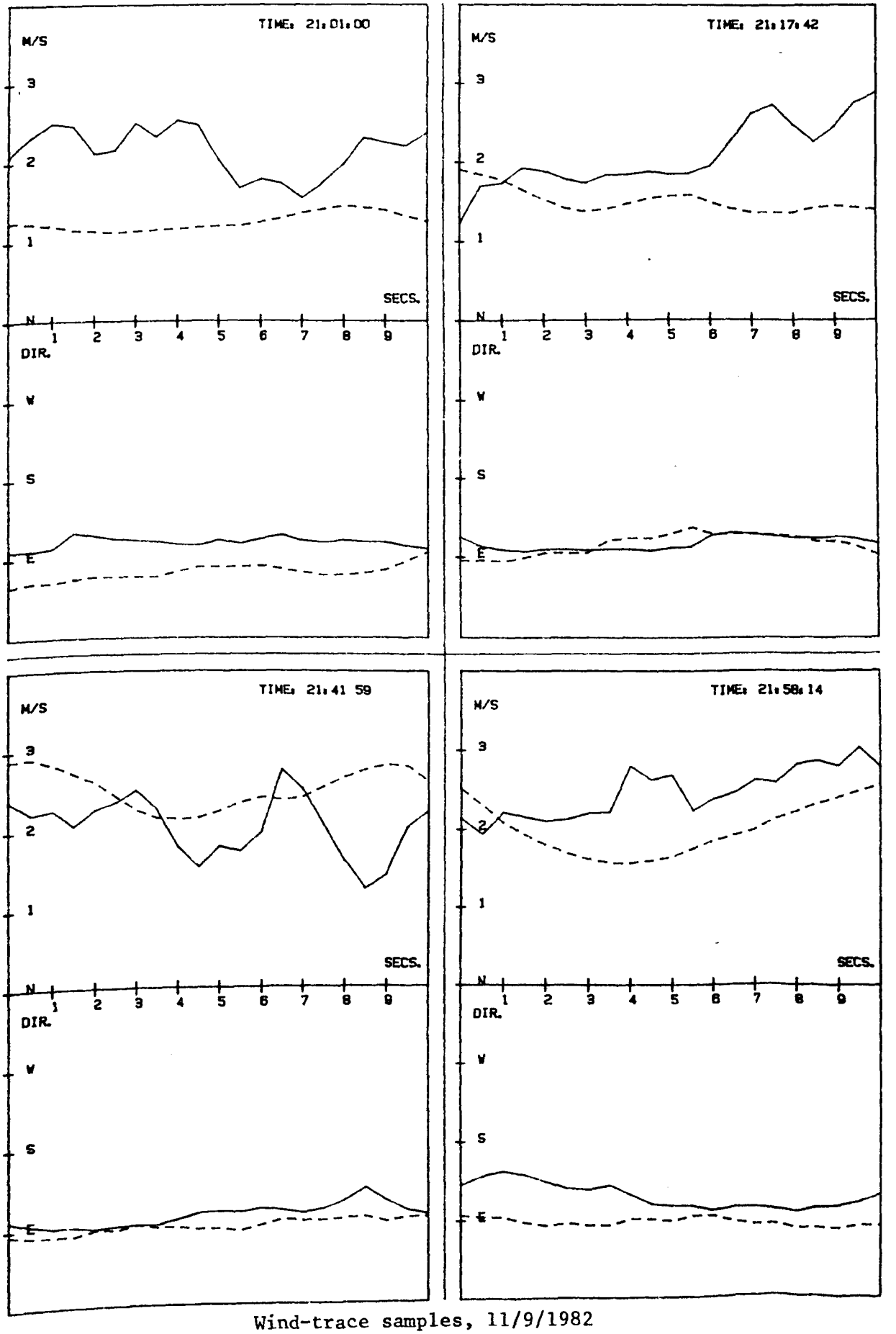

Relative time
W
N
3.61m
S
E
Windspeed: 2.66m/s
Wind Direction: 115°
Time surface Matrix
11.9.1982
21.00-22.00 BST
(ellipse denotes trap)
135°
(compass bearing)

Figure 29



Wind-trace samples, 11/9/1982

Solid line - Lowne vanes. Dashed lines - Porton

Figure 30

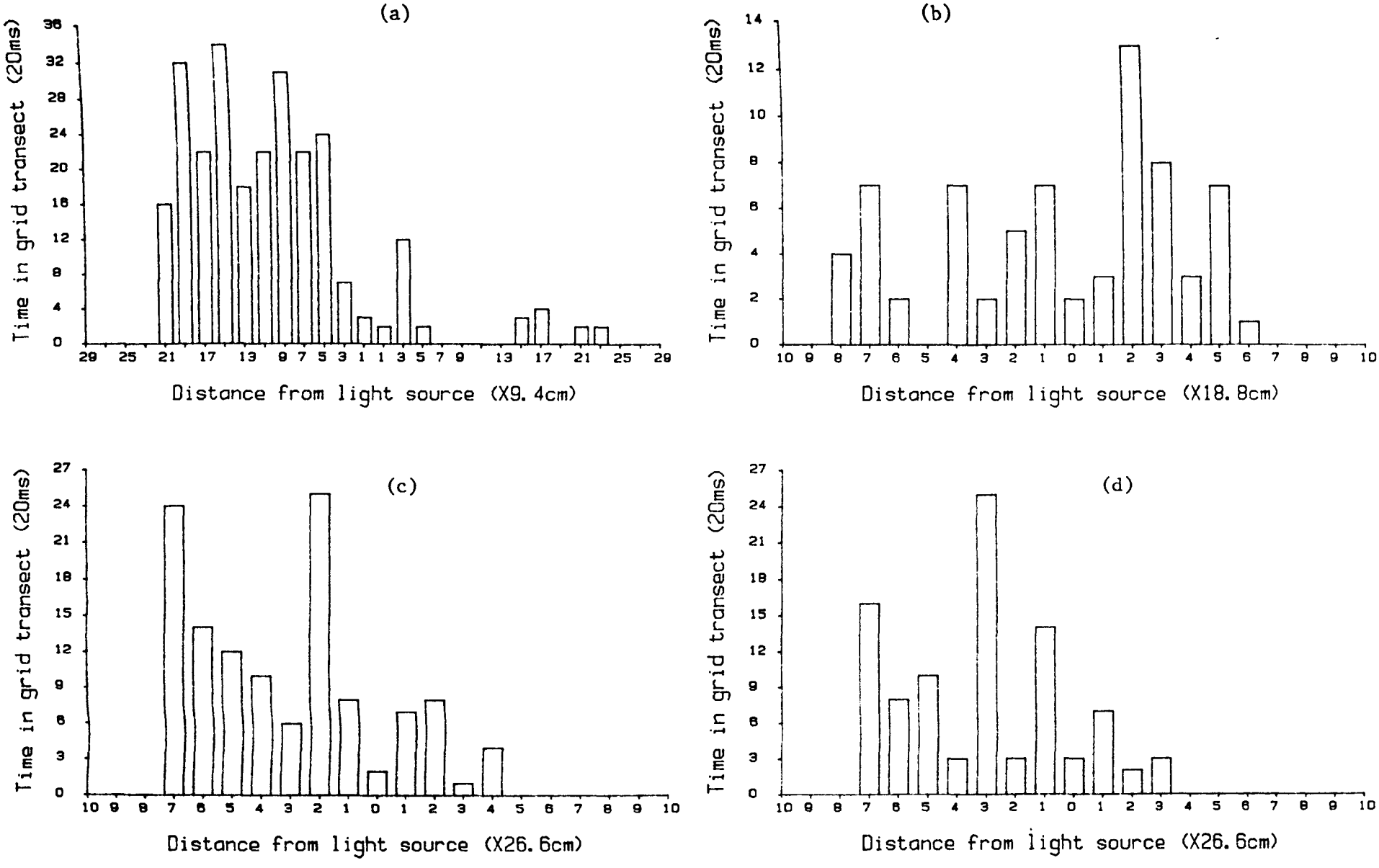


Figure 31

Transects across TSM, 11.9.1982.

a) W/E
b) S/N
c) SW/NE
d) NW/SE

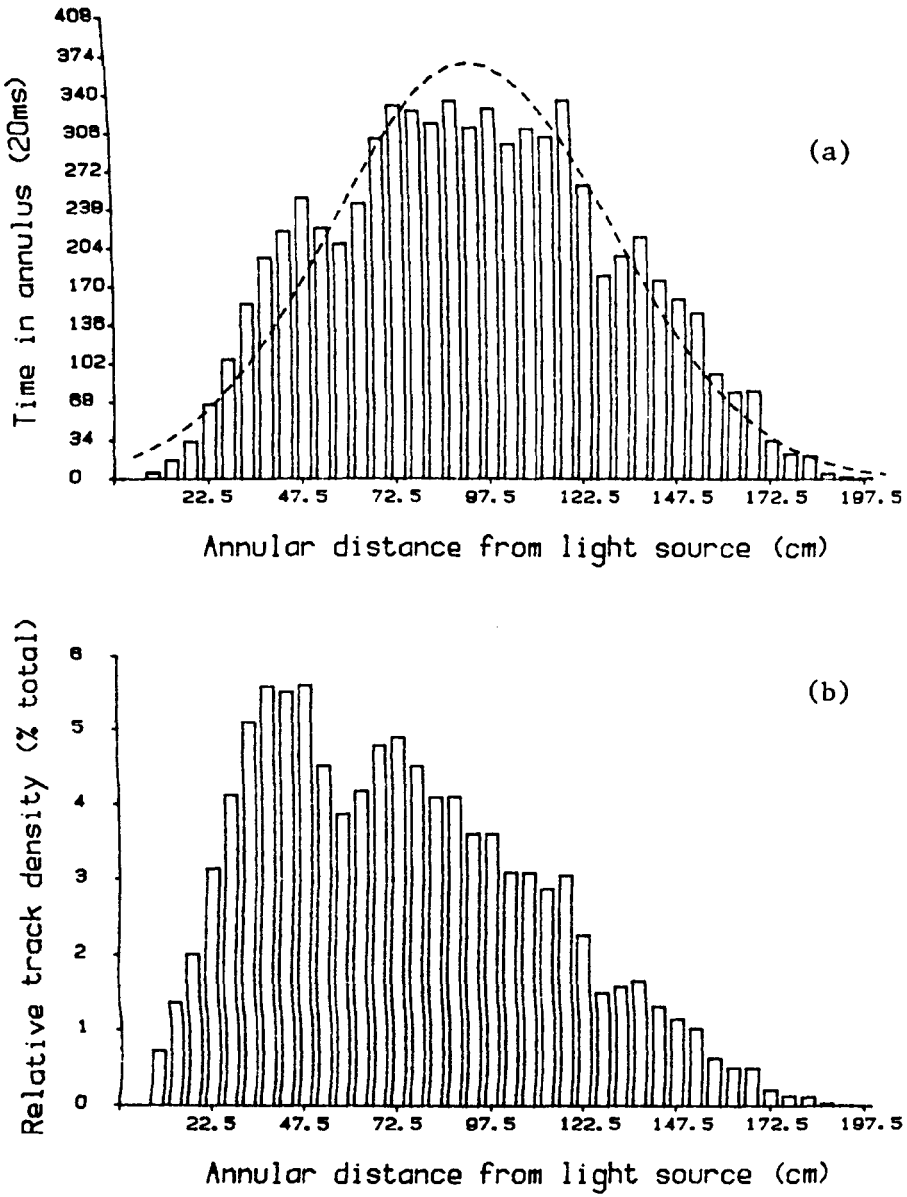


Figure 32

The Derivation of Radial Density.

Although, for the 6.9.1982, the time spent within each successively larger annular area around the lamp (a) appears to follow some ideal Gaussian distribution (dashed line), the true density is calculated by dividing the total time spent in each annulus by its area (b).

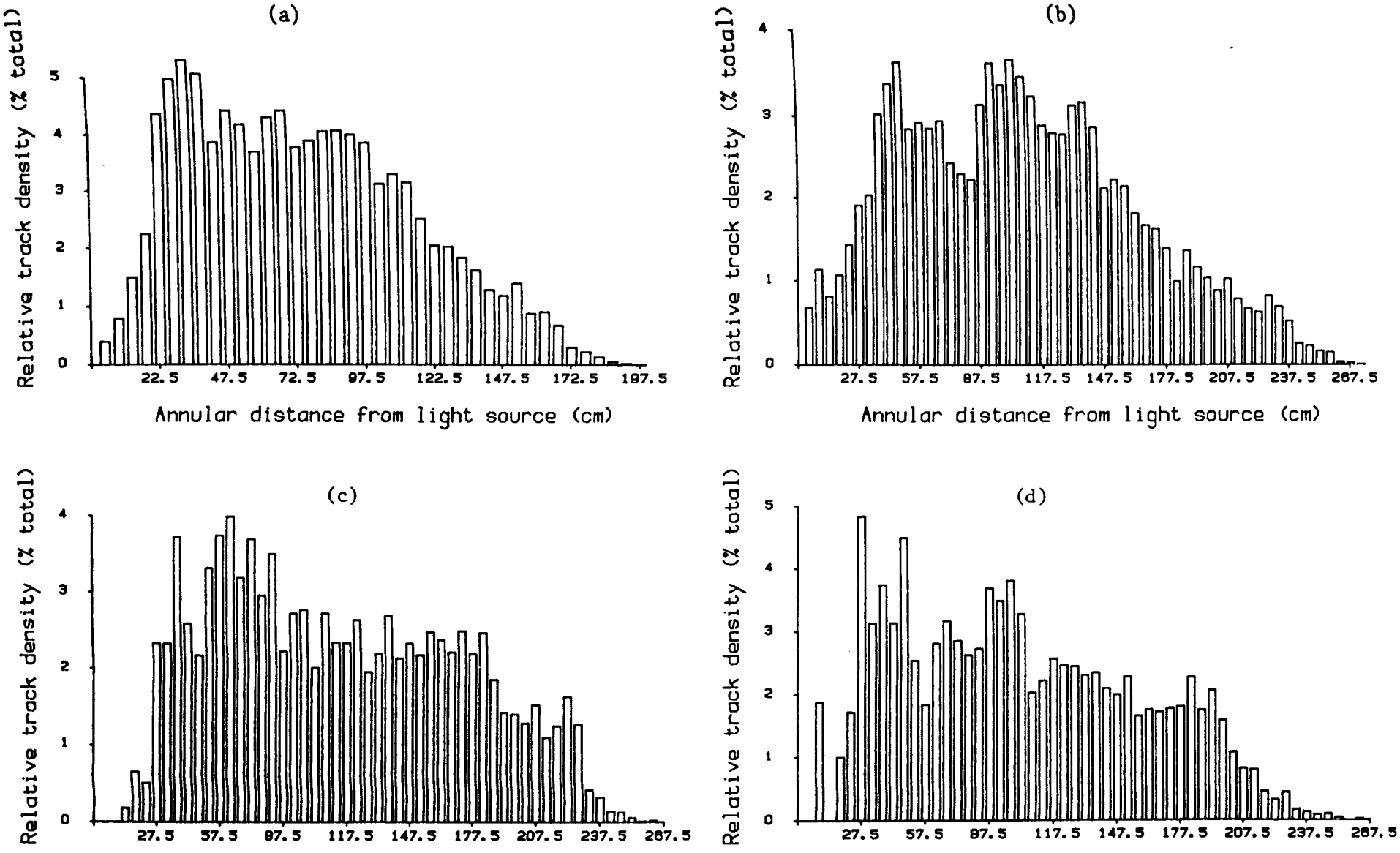


Figure 33

Radial density distributions

a) 8.9.1982 b) 9.9.1982
c) 10.9.1982 d) 11.9.1982

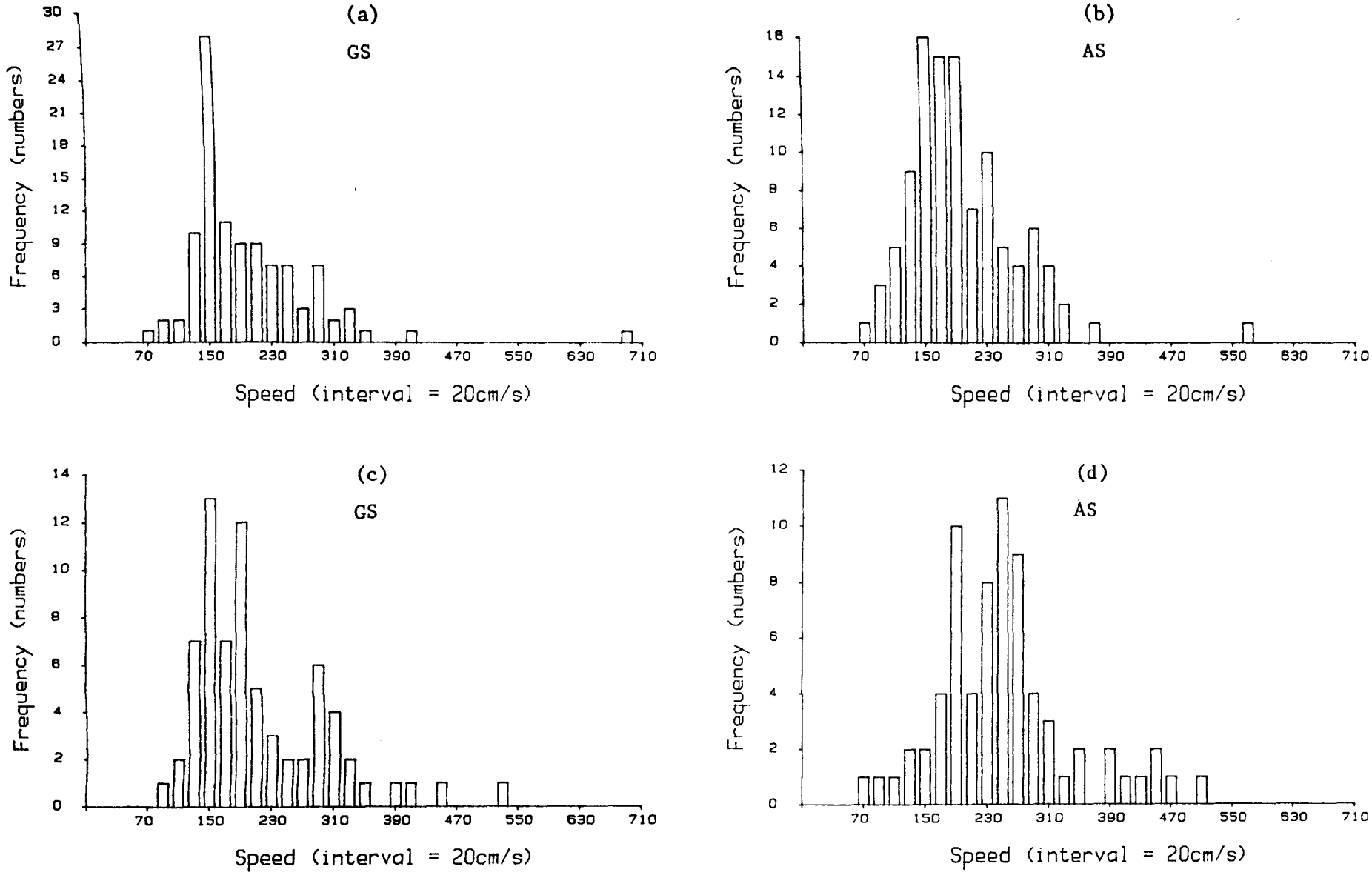


Figure 34

Averaged-mean ground and airspeed frequency distributions for 8.9.1982 (a & b) and 10.9.1982 (c & d)

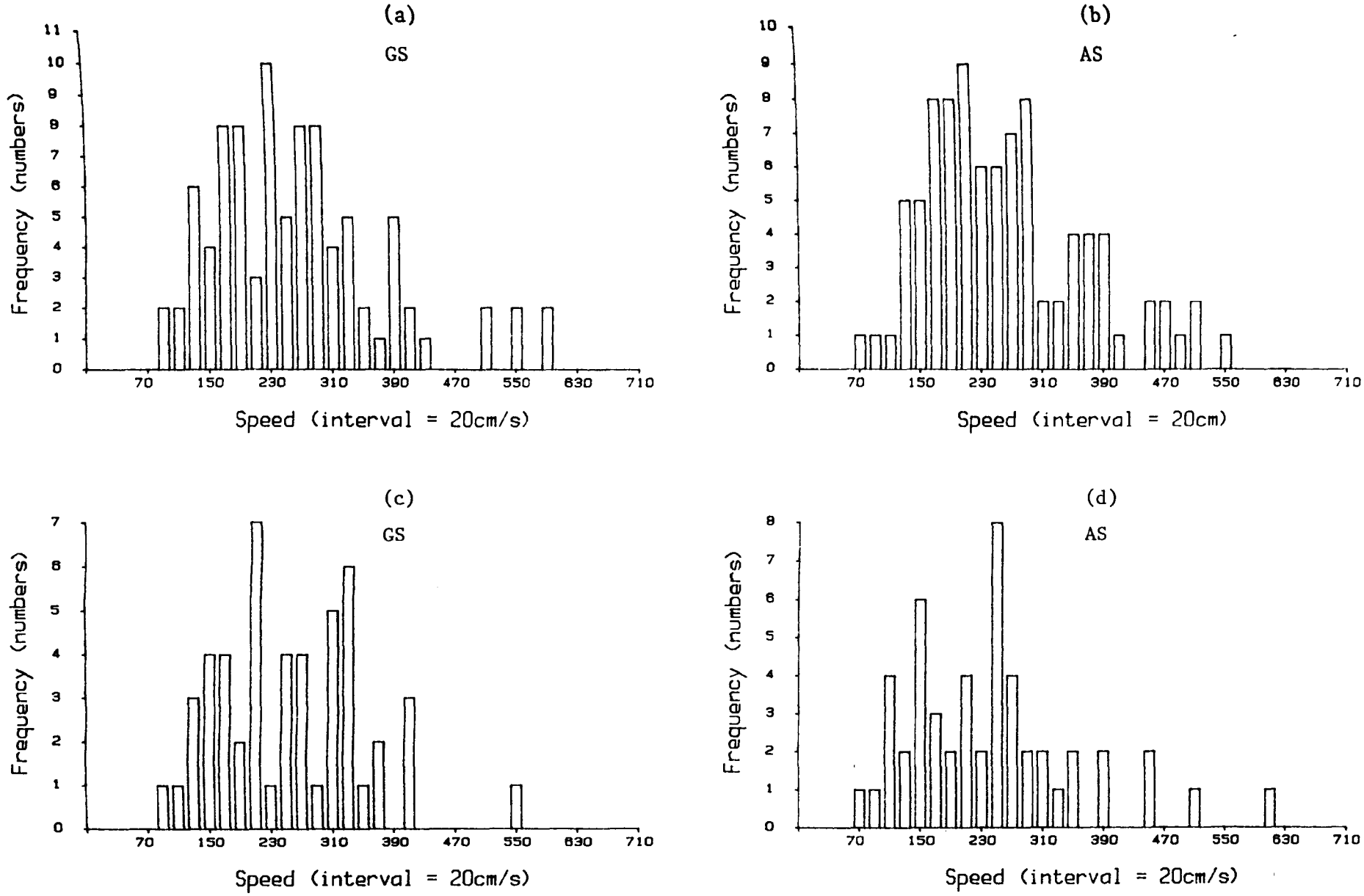
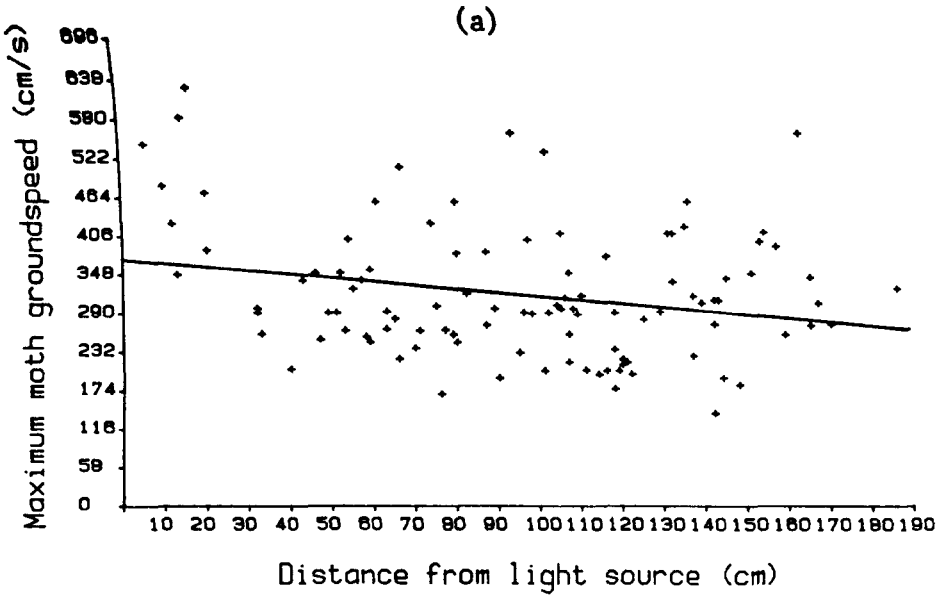
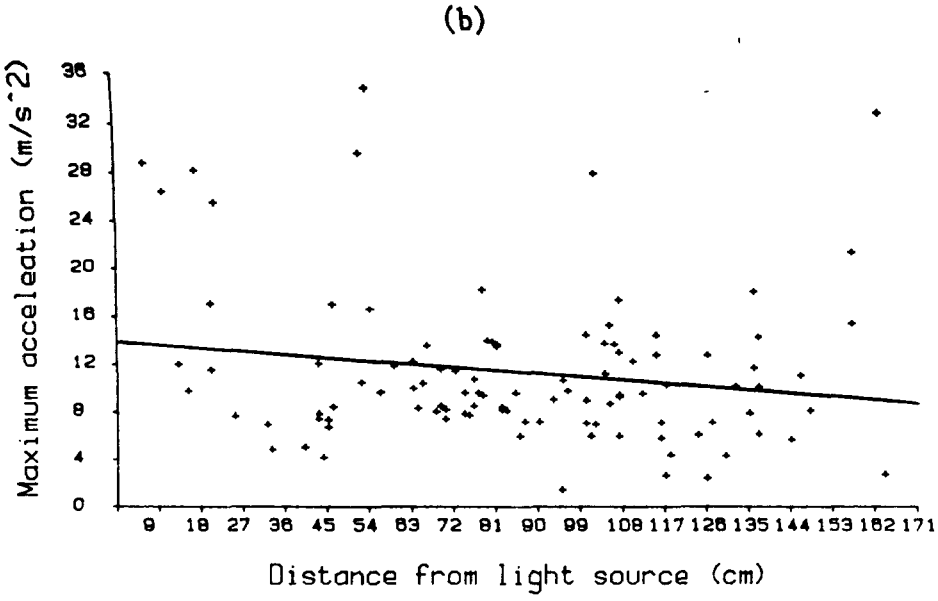


Figure 35

Averaged-mean ground and airspeed frequency distributions for 9.9.1982 (a & b) and 11.9.1982 (c & d).





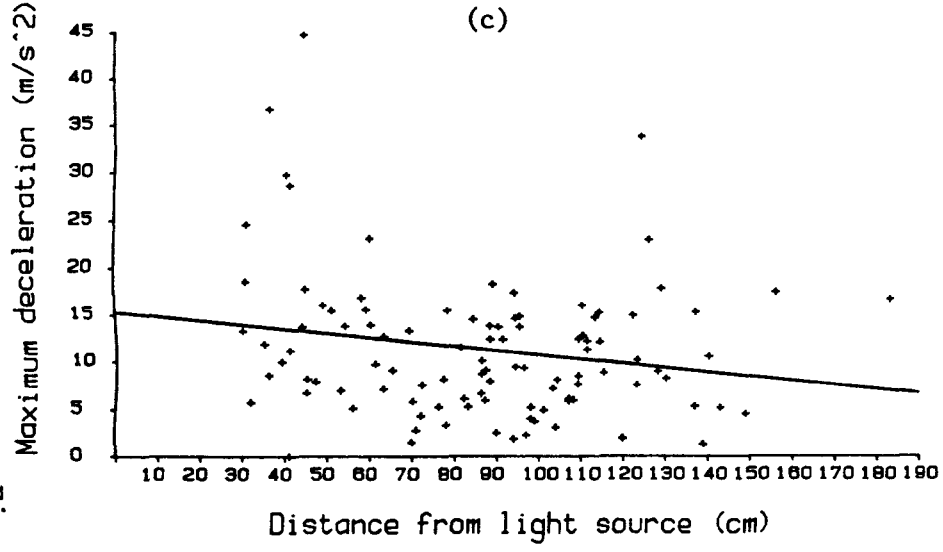


Figure 36

Scattergrams indicating inverse relationships between distance from the light source, and averaged-maximum groundspeeds, accelerations decelerations (6.9.1982).

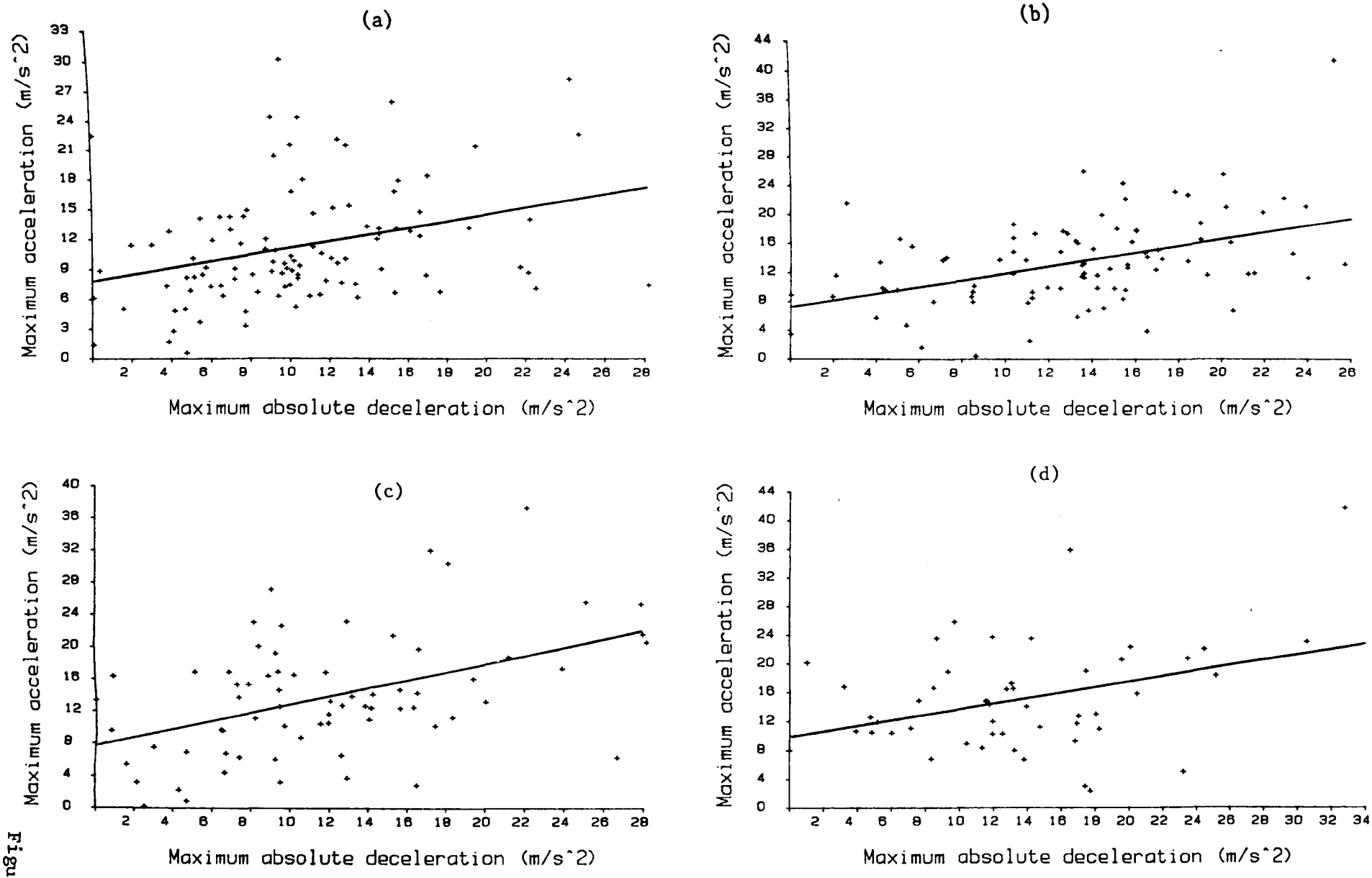


Figure 37

Relationship between averaged maximum acceleration and deceleration.

a) 8.9.1982 b) 9.9.1982
c) 10.9.1982 d) 11.9.1982

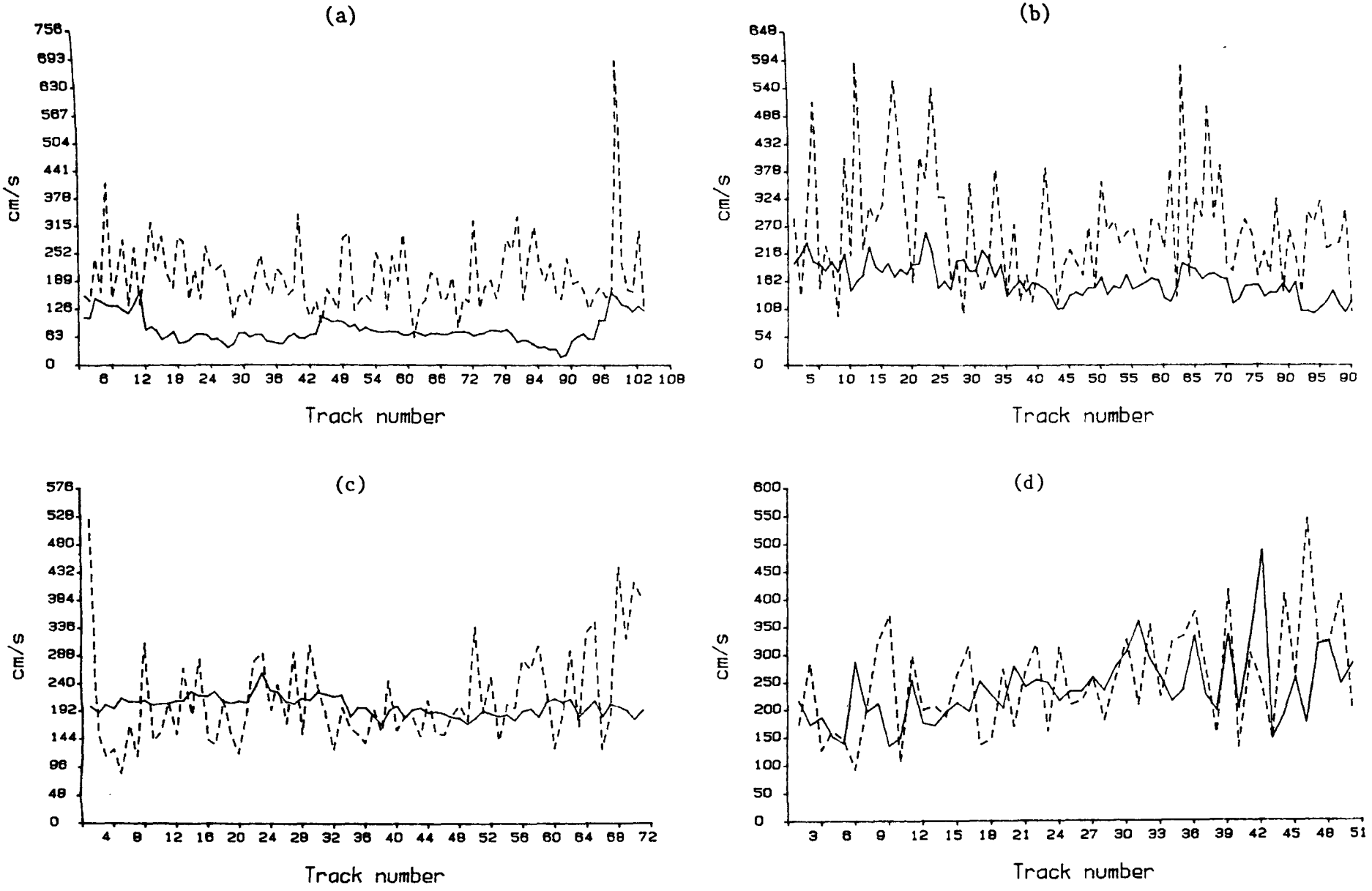


Figure 38

Moth groundspeeds (dashed lines) and corresponding windspeeds (solid line).

a) 8.9.1982 b) 9.9.1982
c) 10.9.1982 d) 11.9.1982

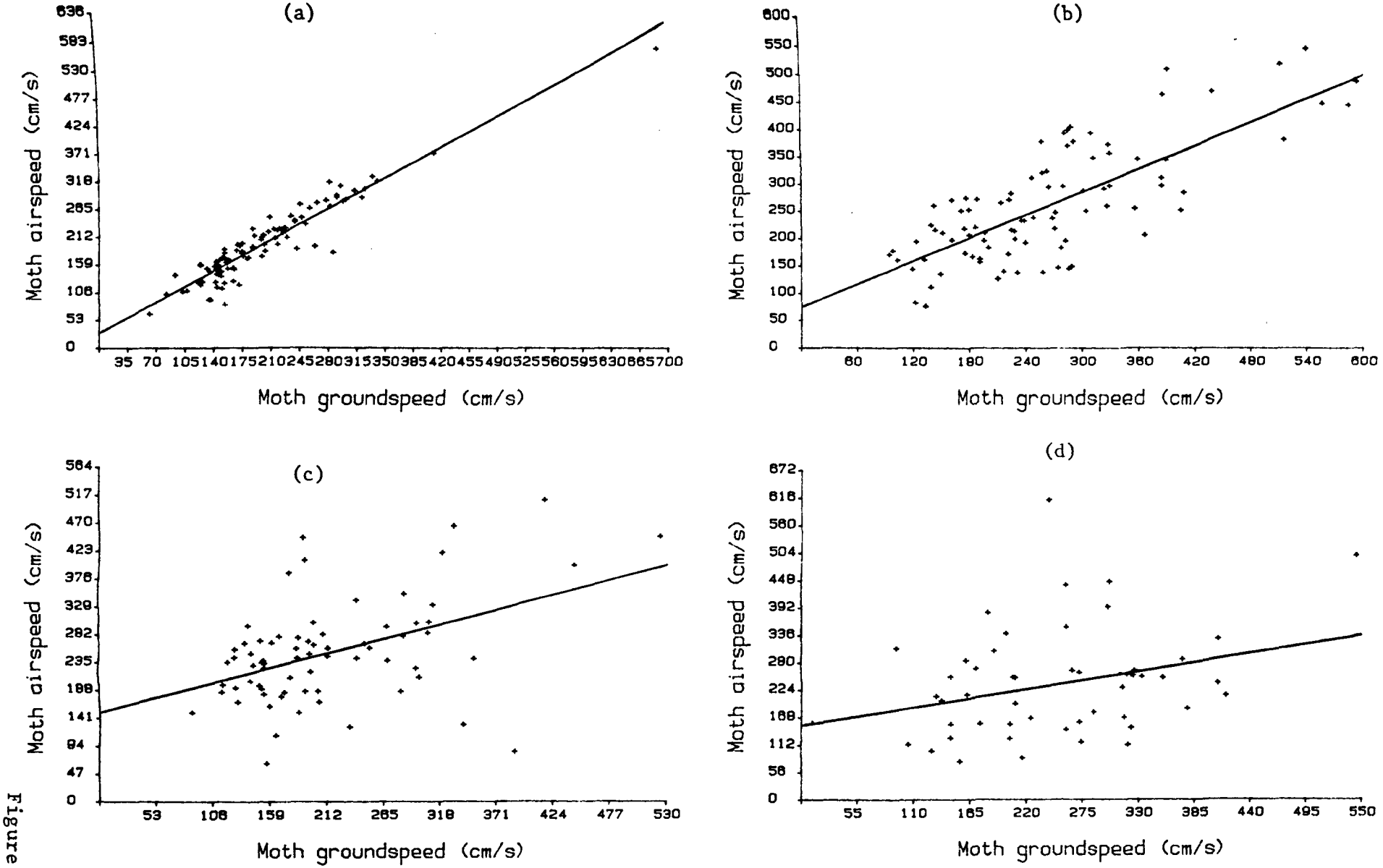
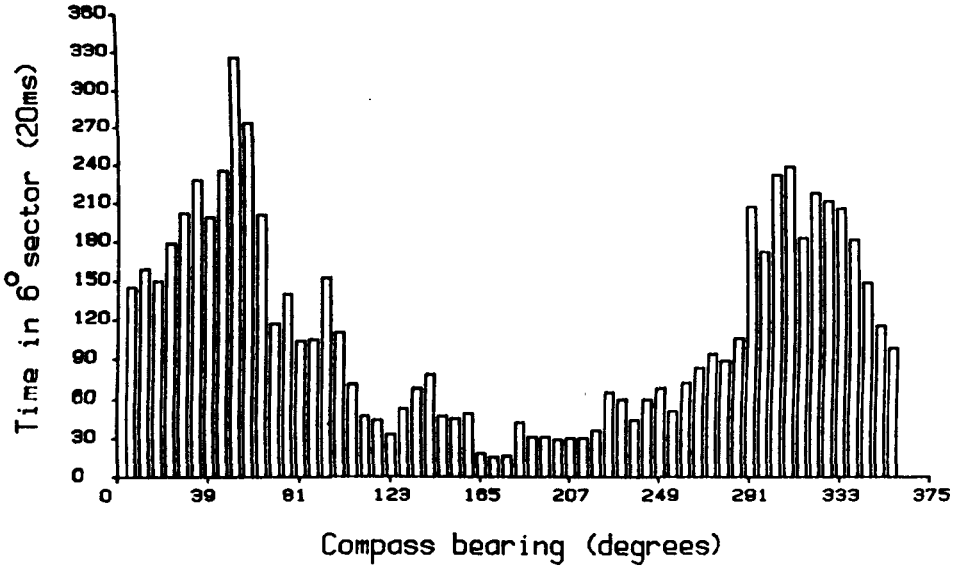


Figure 39

Relationship between averaged-mean air and groundspeeds.

a) 8.9.1982 b) 9.9.1982
c) 10.9.1982 d) 11.9.1982



Angular density (moth) distributions for 6.9.1982, using a scan-resolution of 6^{o}. Note the symmetrical pattern with respect to wind direction, originating from 188.5^{o}.

Figure 40

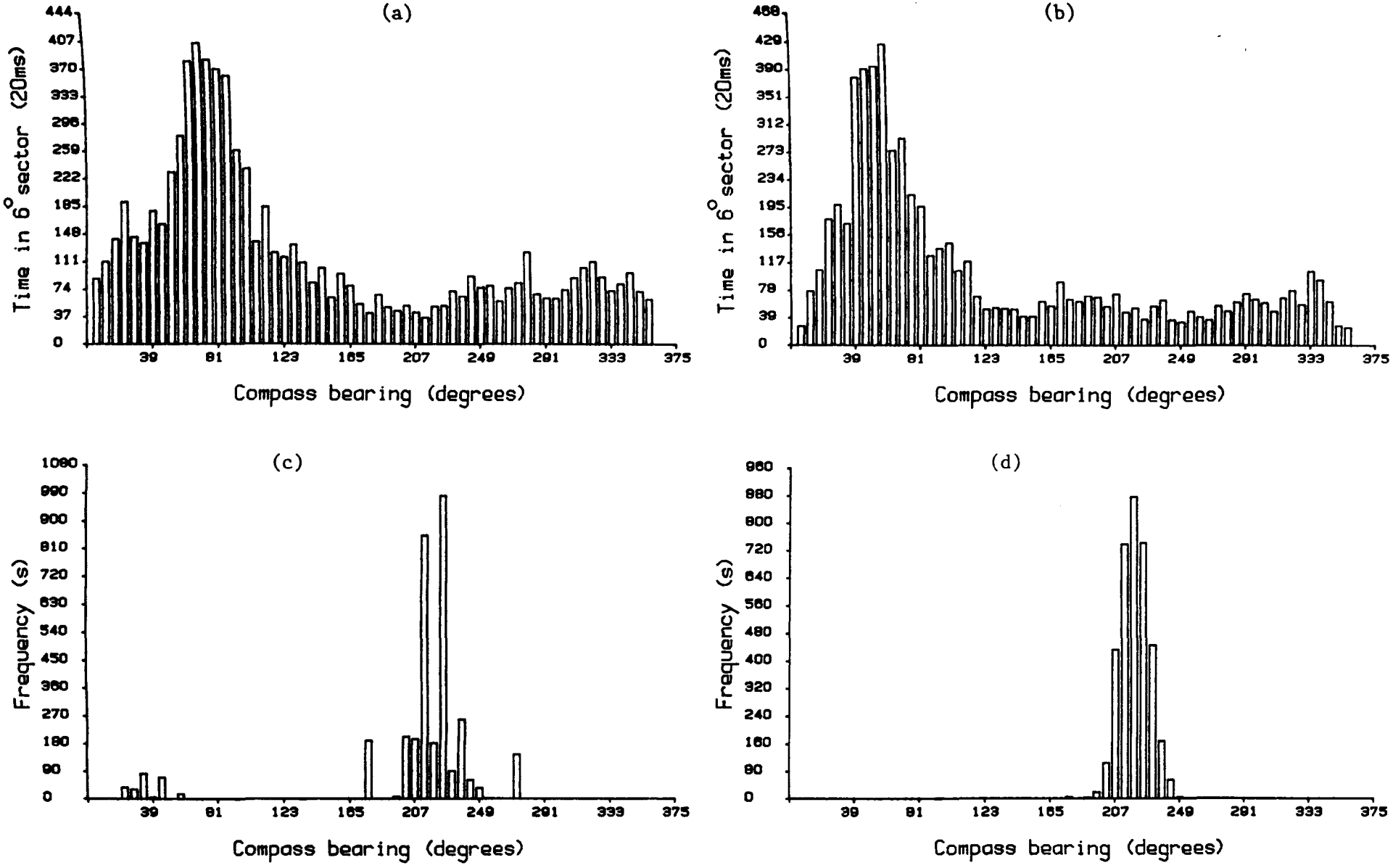


Figure 41

Angular density distributions for 8.9.1982 and 9.9.1982 (a & b) and the corresponding linear wind-rose histograms (c & d).

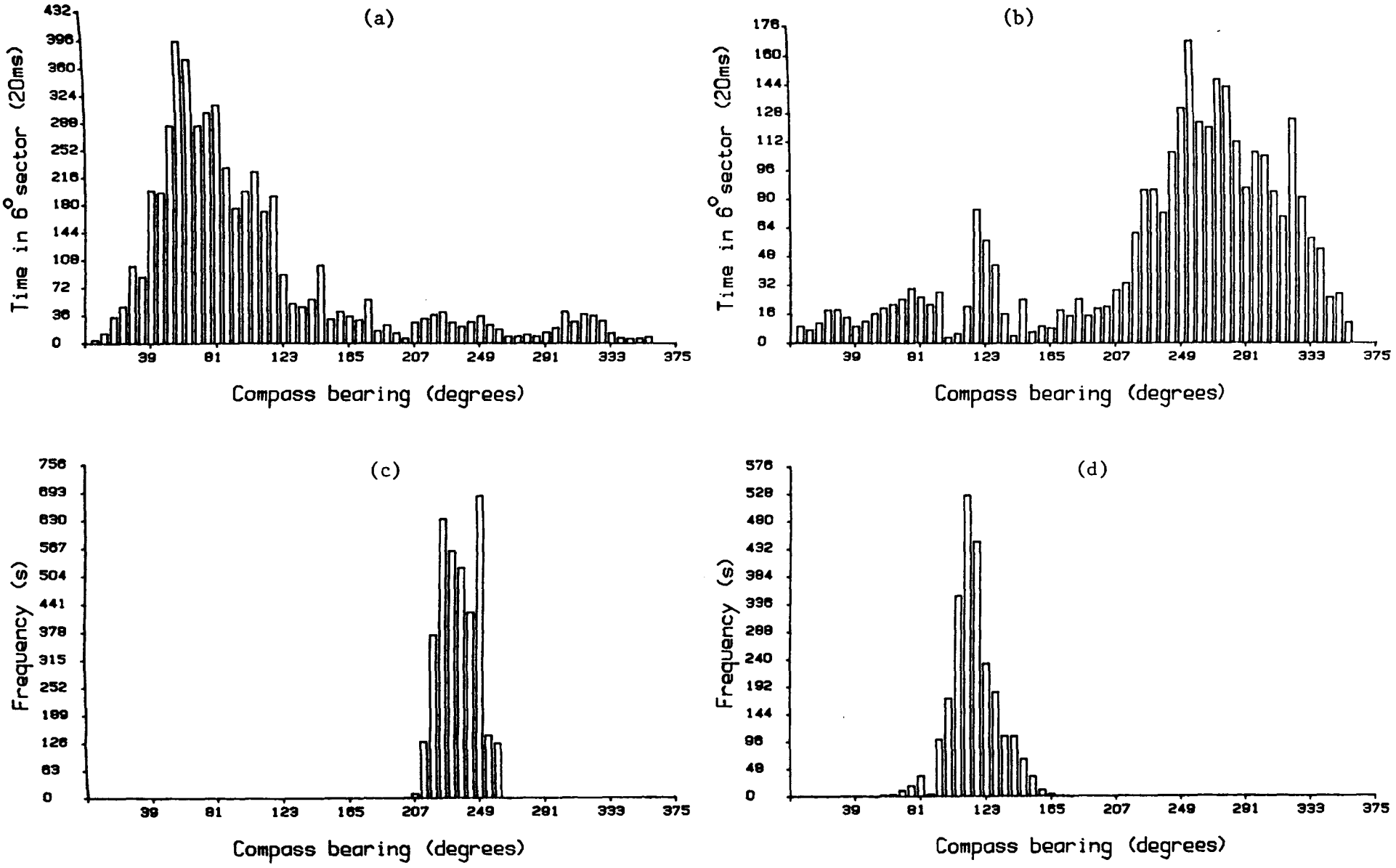


Figure 42

Angular density distributions for 10.9.1982 and 11.9.1982 (a & b) and the corresponding linear wind-rose histograms (c & d).

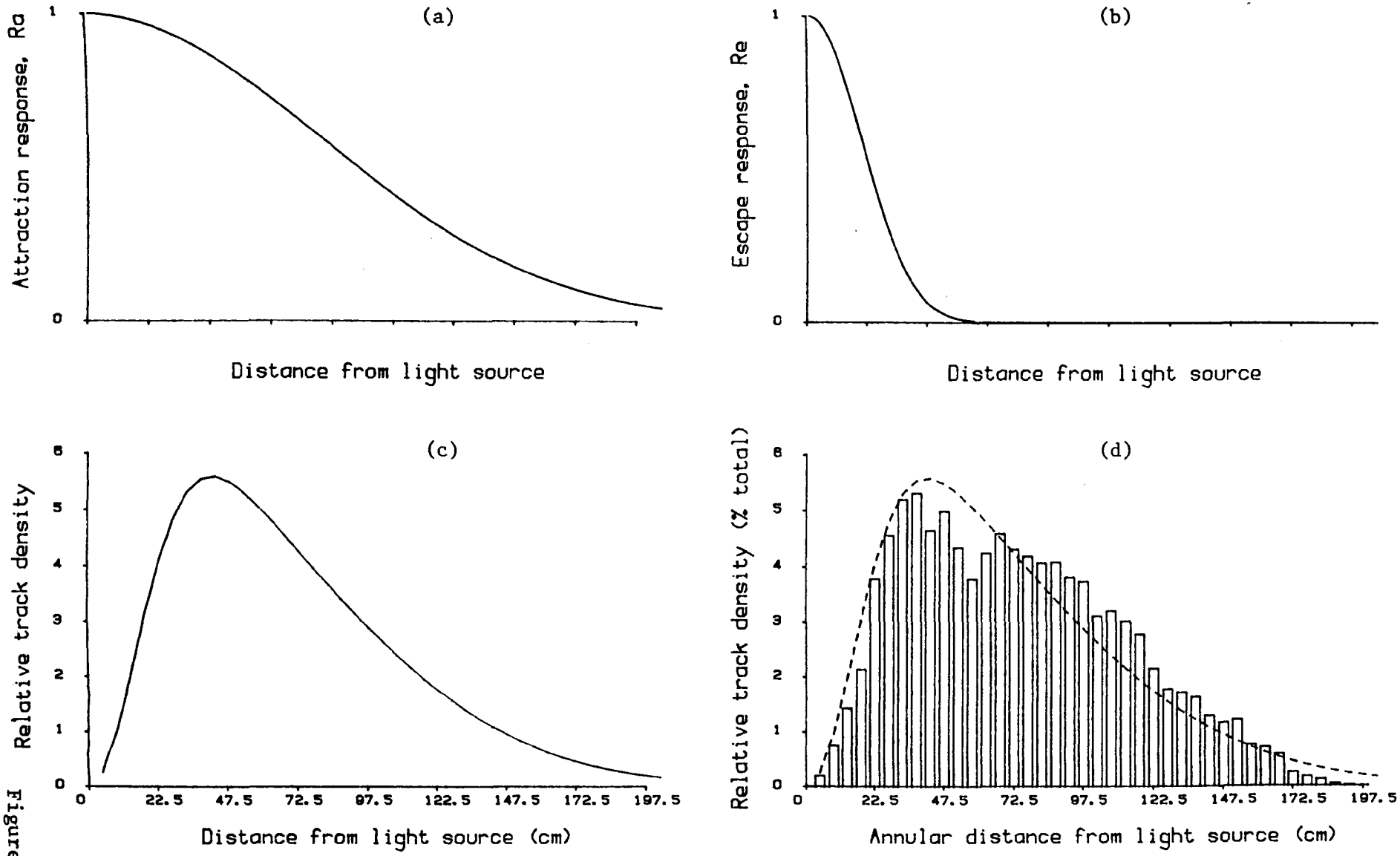
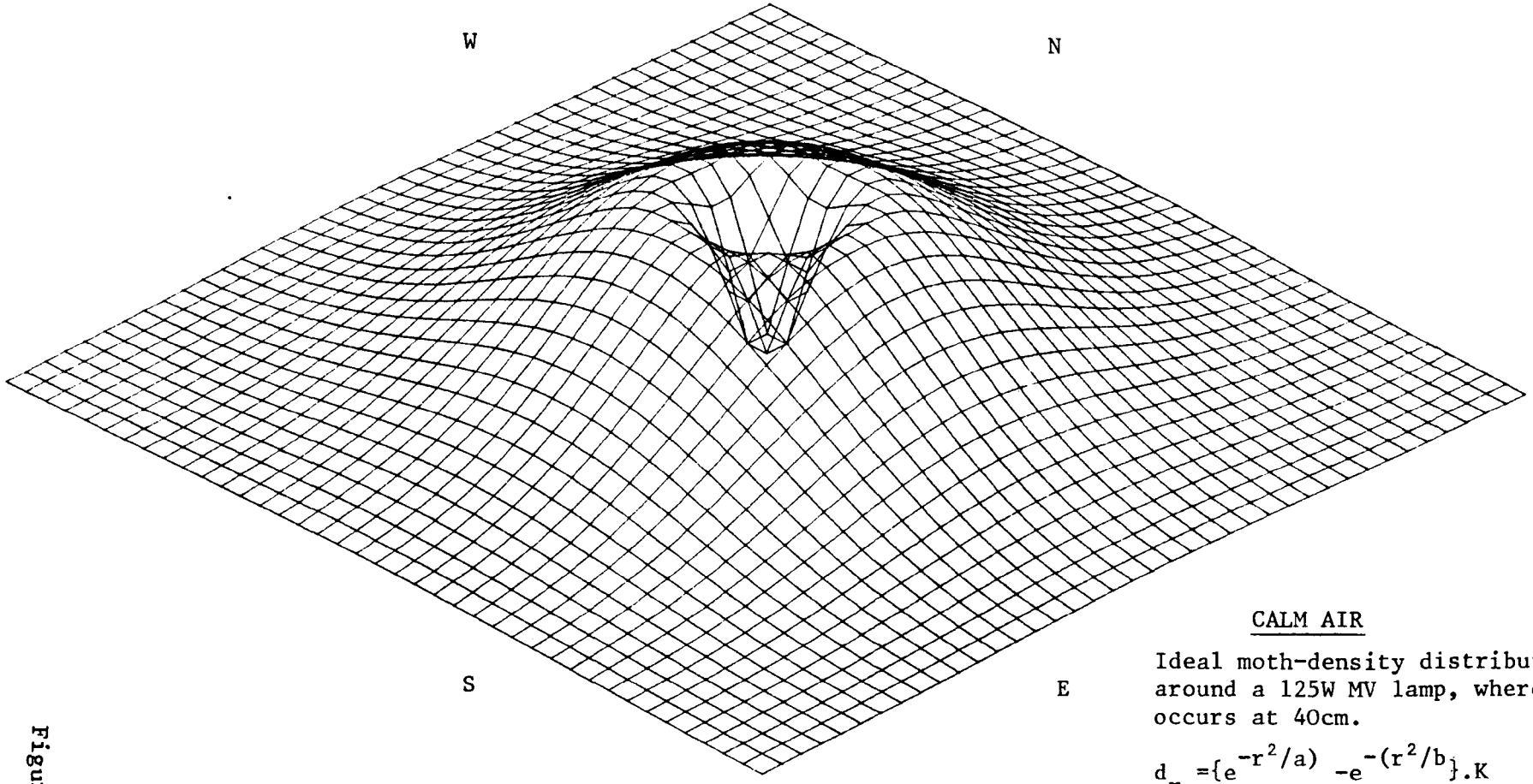


Figure 43

The escape response, R_e(b), is subtracted from the attraction response, R_a (a), to give the ideal distribution of (c). In (d) it is overlayed with the accumulated data of the 6/9 and 8/9, 1982.



CALM AIR

Ideal moth-density distribution around a 125W MV lamp, where d_{max} occurs at 40cm.

$$d_r = \{e^{-r^2/a)} - e^{-(r^2/b}\}.K$$

Figure 44

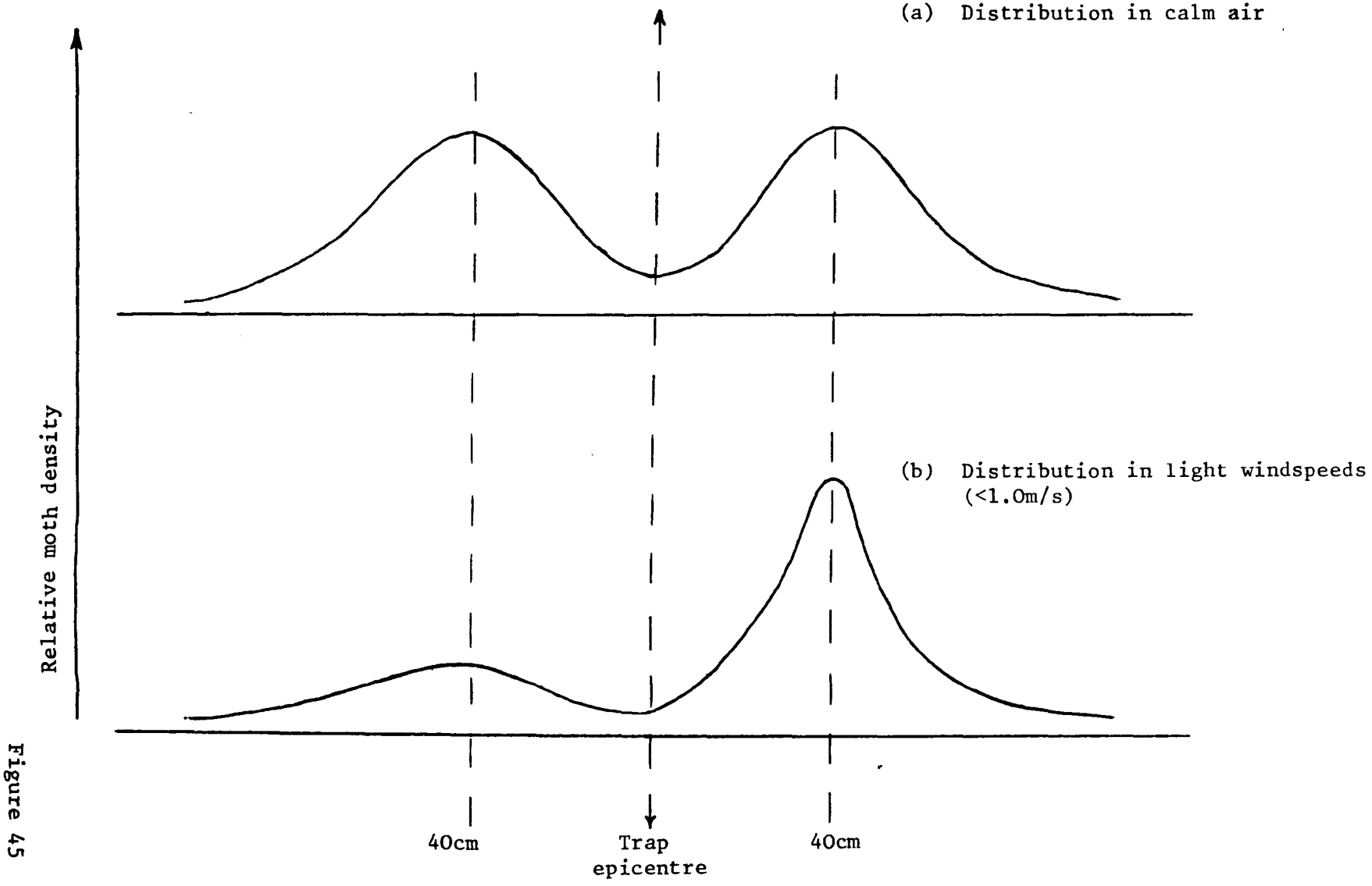

(a) Distribution in calm air
Relative moth density
(b) Distribution in light windspeeds
(<1.0m/s)
40cm
Trap
epicentre
40cm

Figure 45

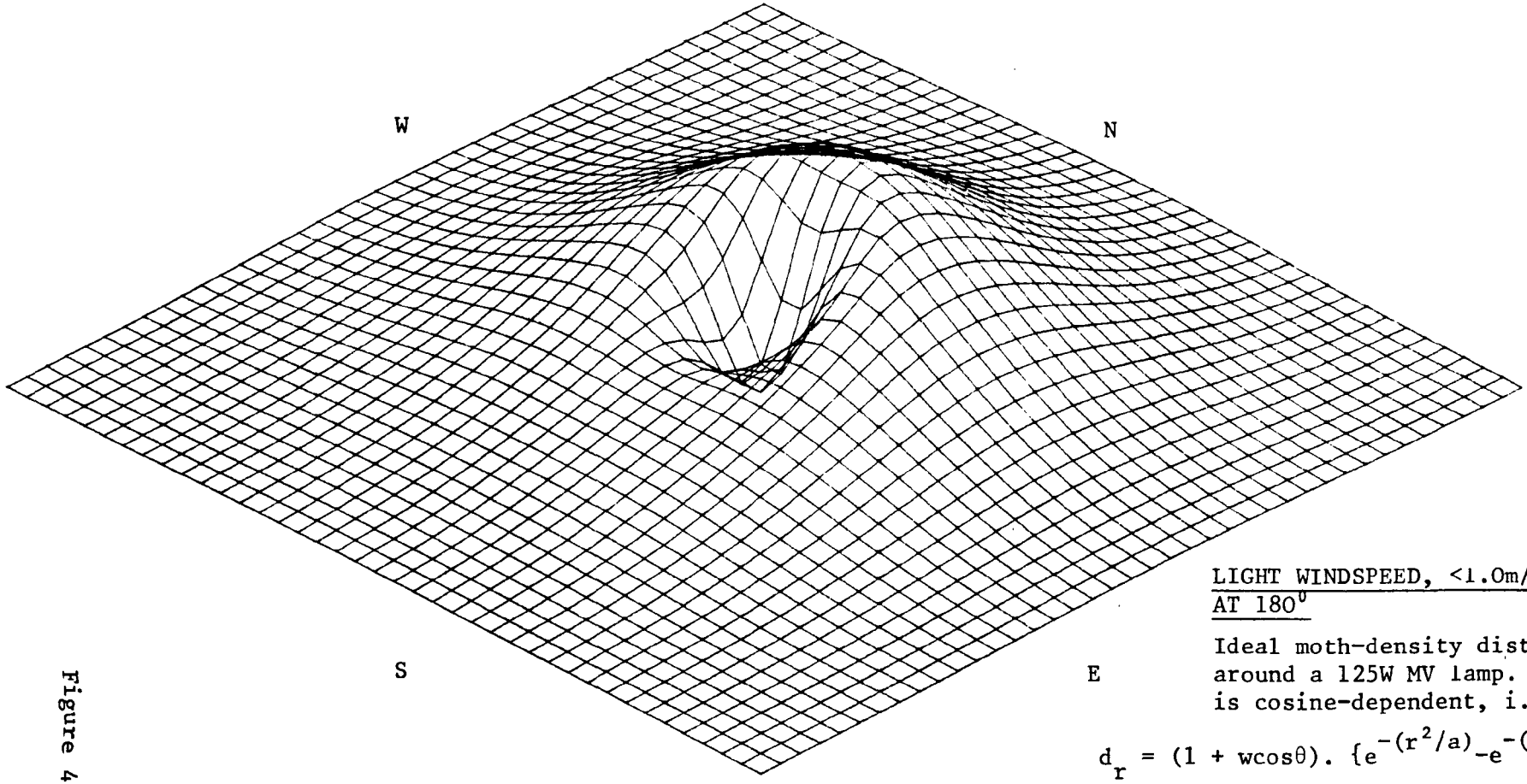


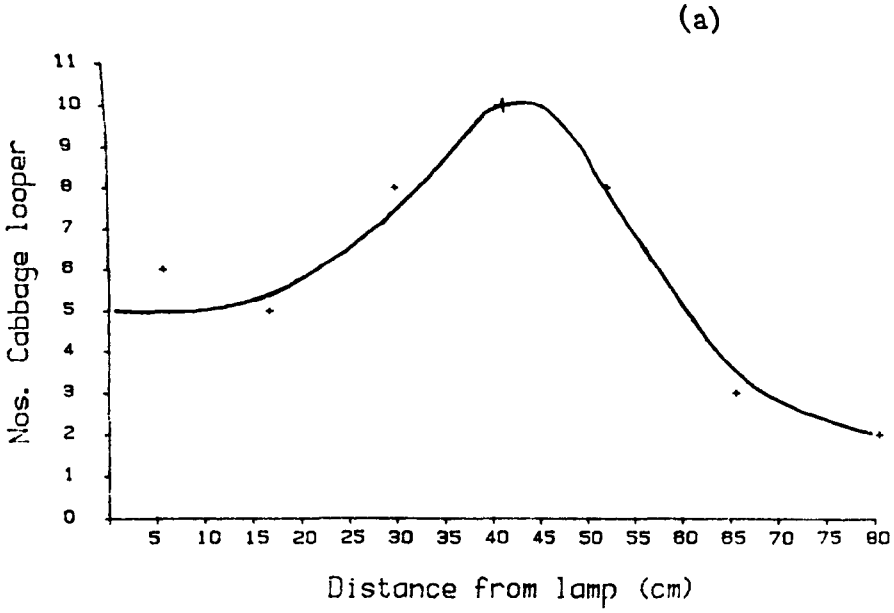
Figure 46

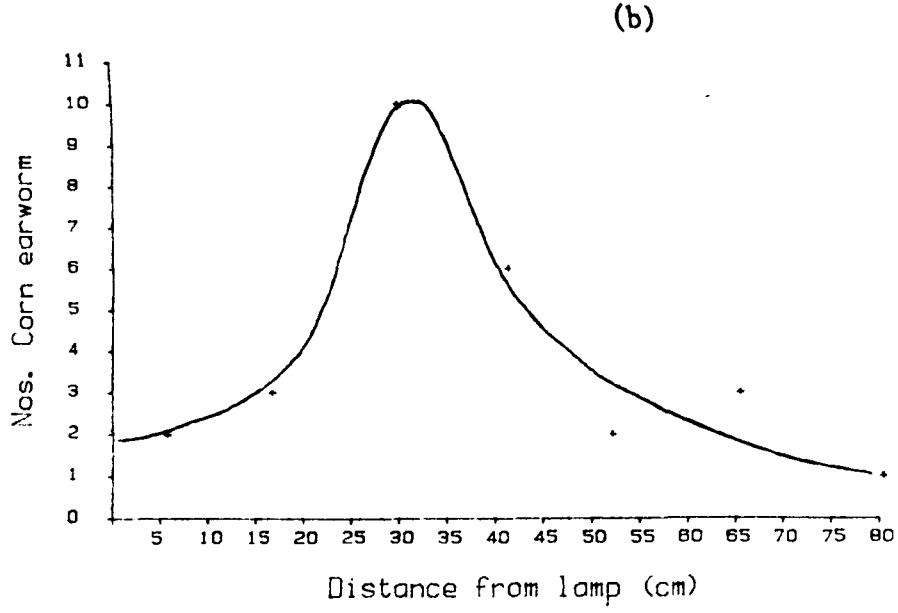
LIGHT WINDSPEED, <1.0m/s
AT 180°

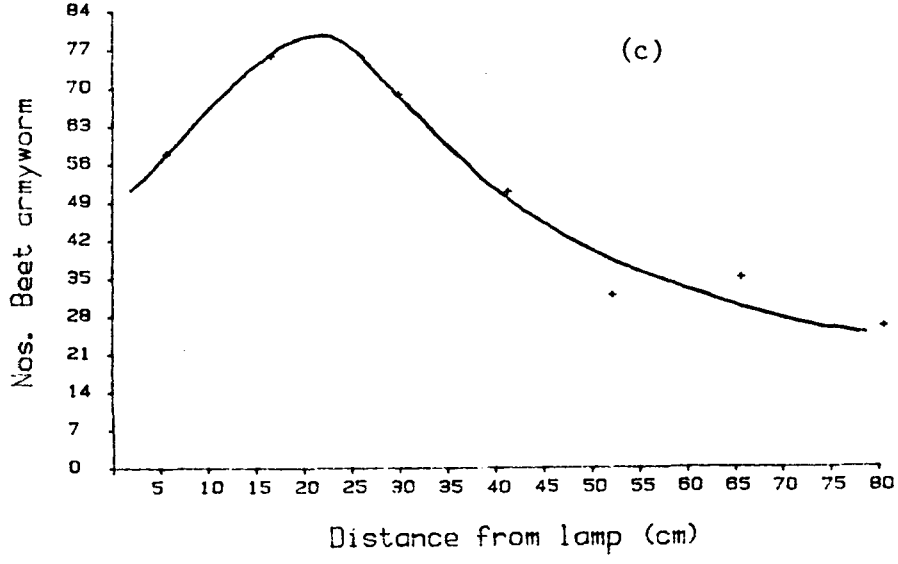
Ideal moth-density distribution around a 125W MV lamp. Density is cosine-dependent, i.e.

$d_r = (1 + w\cos\theta) . \{e^{-(r^2/a)} - e^{-(r^2/b)}\} . K$

d_{max} again occurs at 40cm.







Distributions of the numbers of 3 Lepidopterous species striking baffles radiating from a 15W blacklight, in an open field, as a function of distance from the lamp.
(Redrawn from Hsiao, 1973).

Figure 47

Fieldwork configuration (1983), used to estimate aerial moth density.

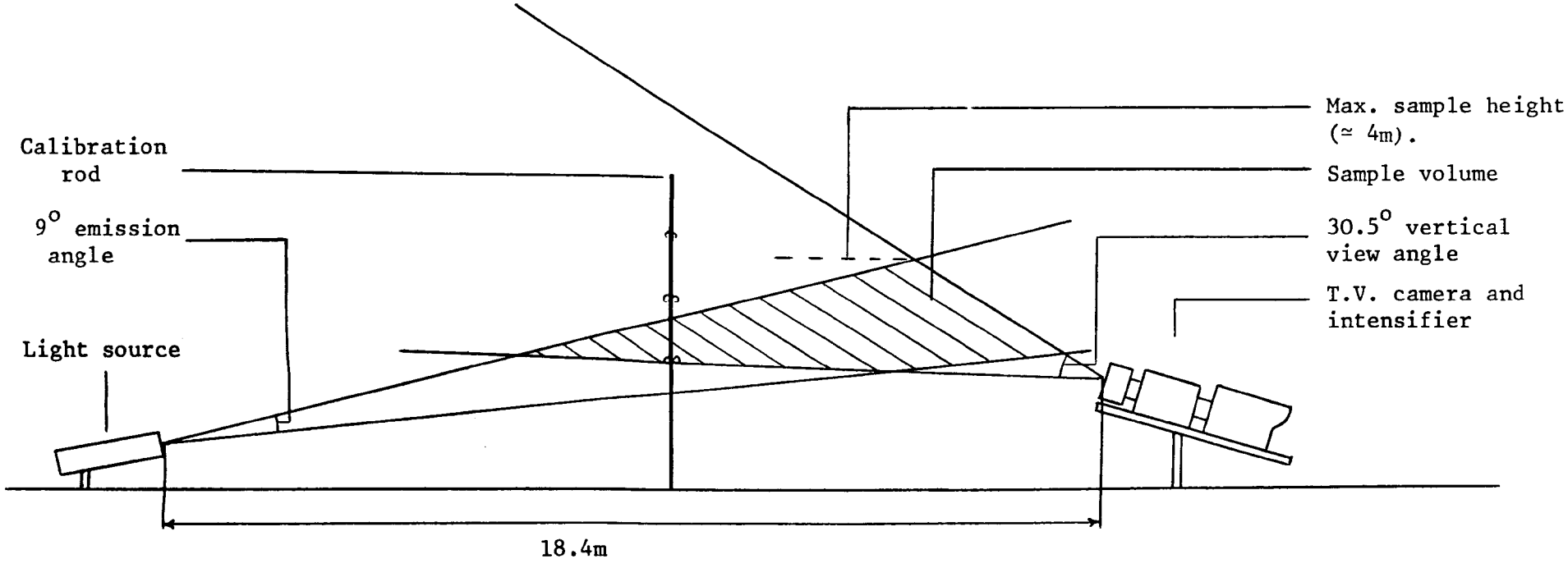
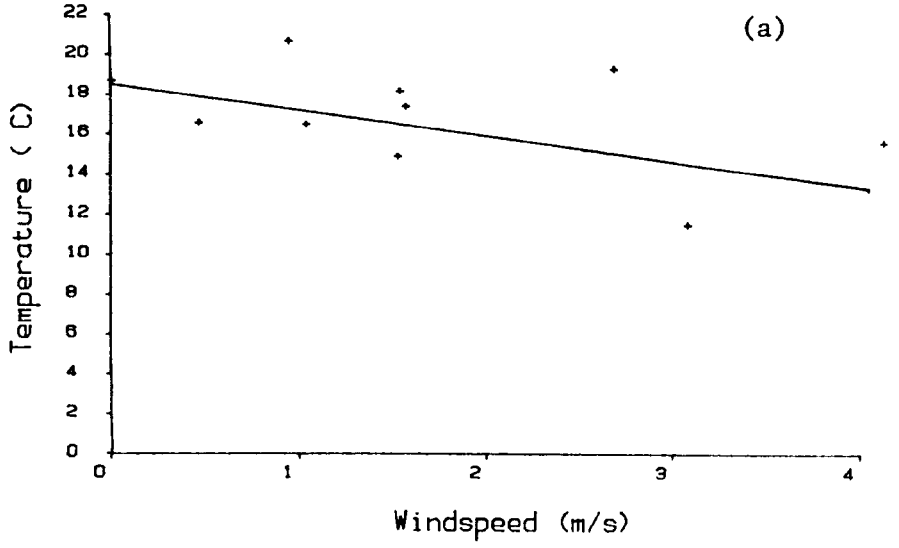
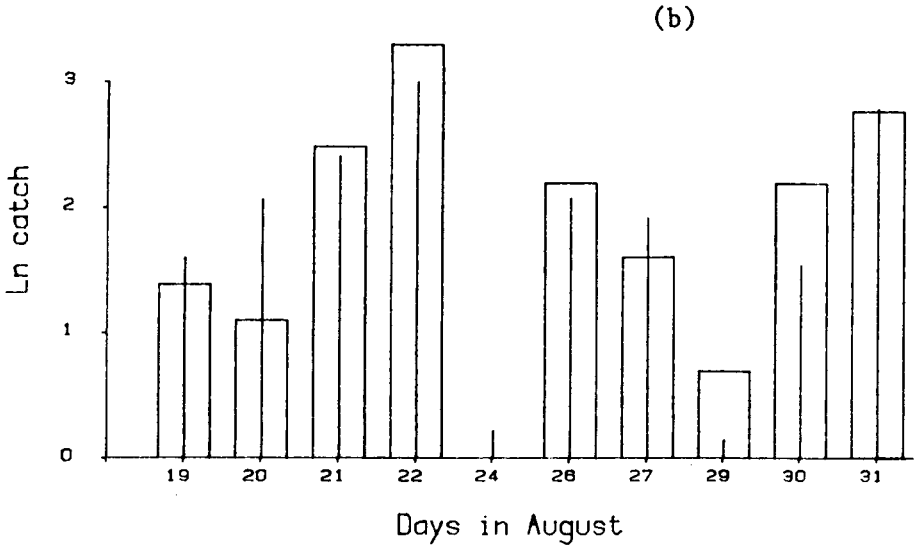
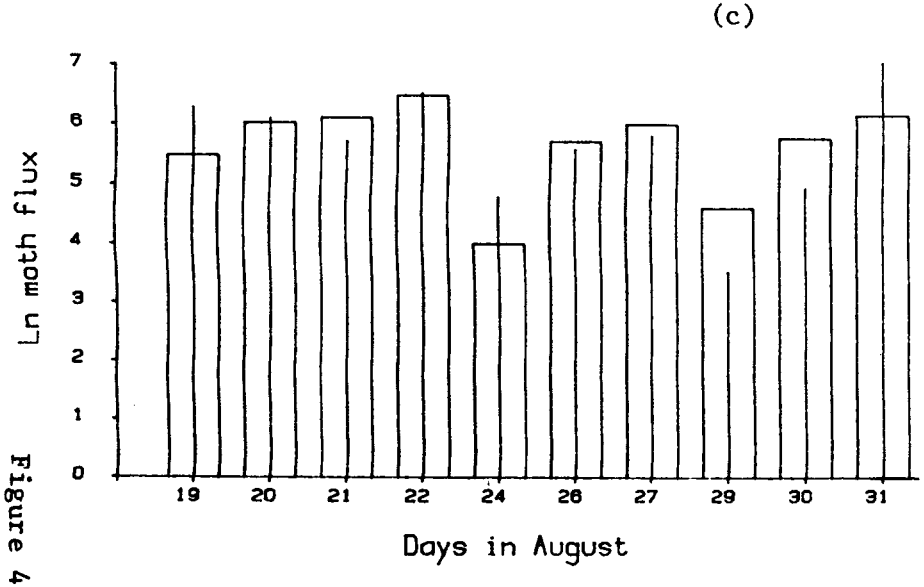


Figure 48







1983

a) Mean temperature as a function of windspeed, during sample period.

b) Total Ln catch in trap at 1.4m, overlayed with expected (solid lines).

c) Ln. moth flux (per $100m^2/h$), overlayed with expected (solid lines).

Figure 49

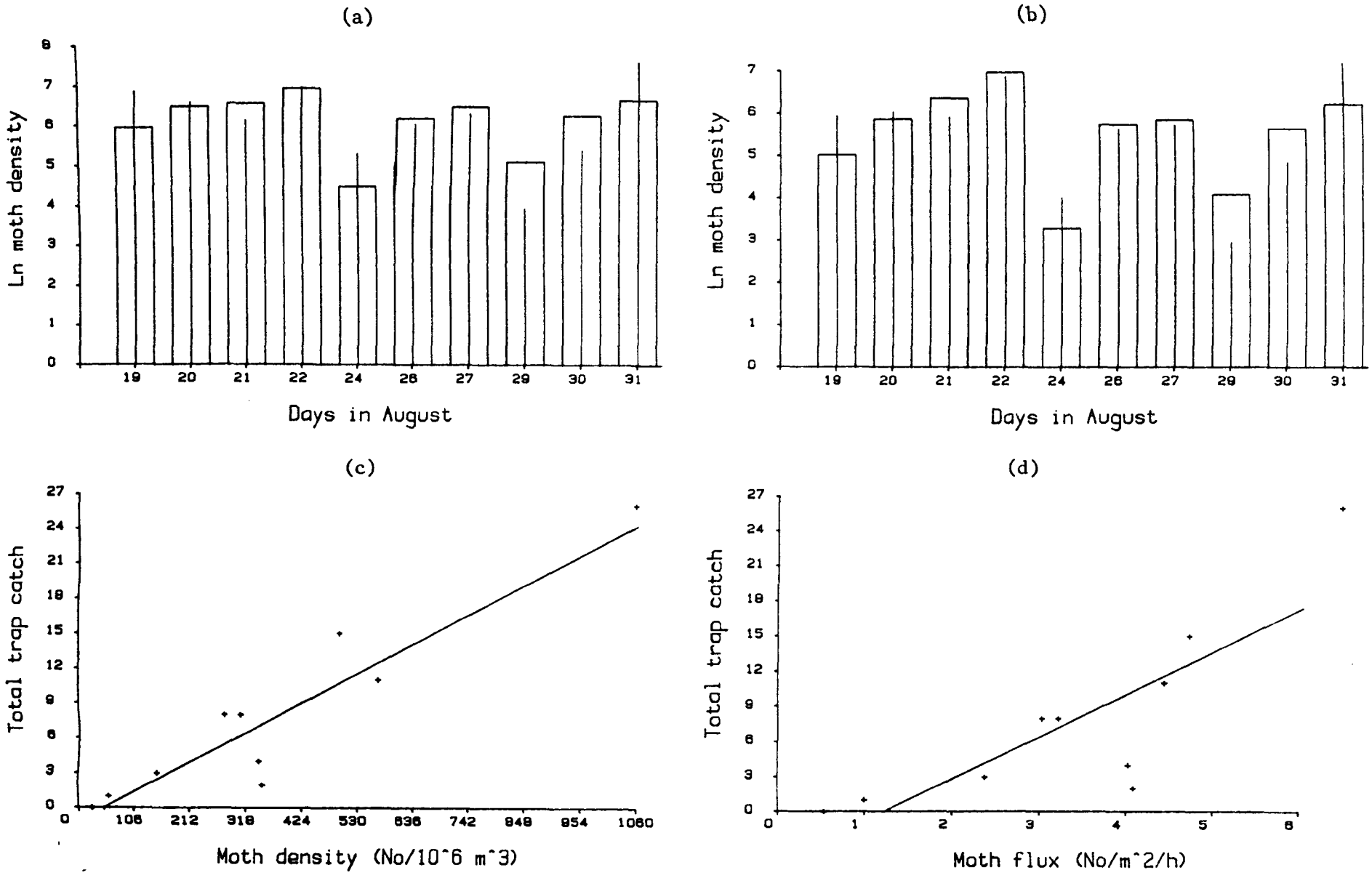
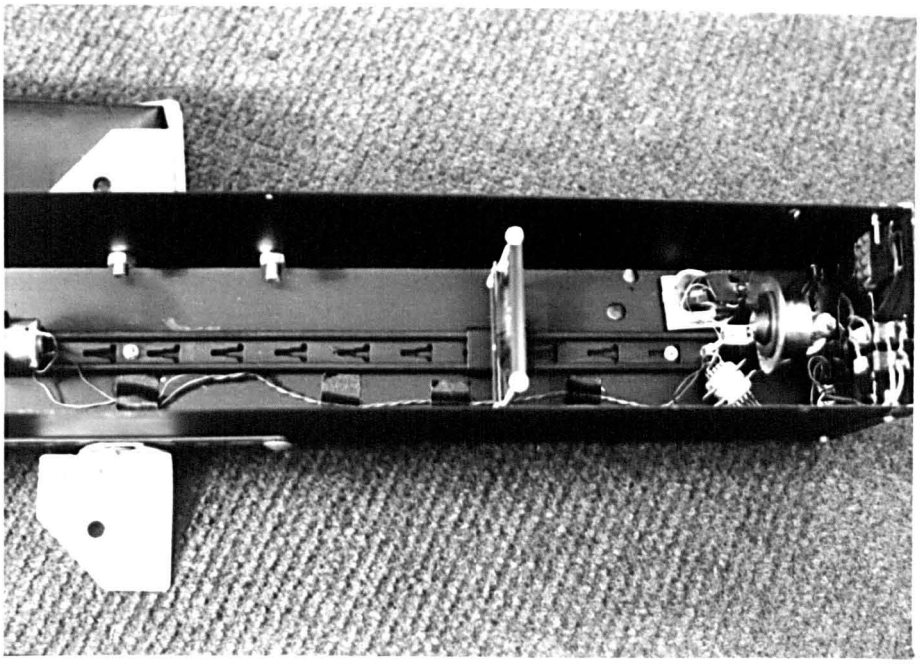
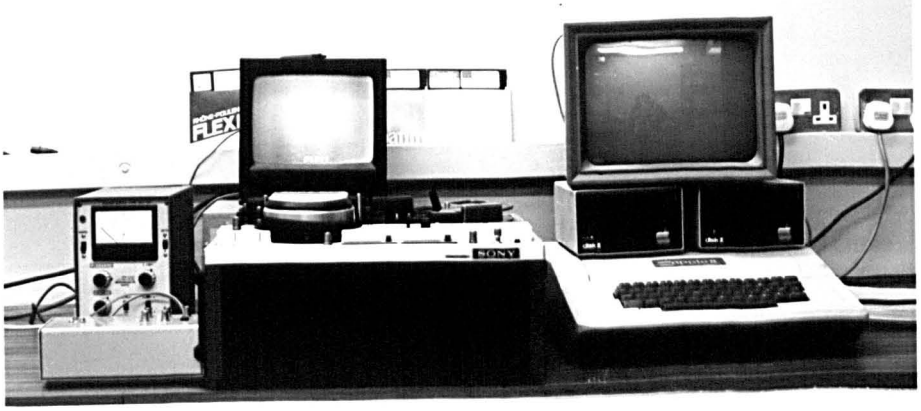


Figure 50

(a) & (b): Ln. density estimates calculated from methods (1) and (3) respectively (see text), overlayed with expected values (solid lines). Units are Ln. No/$10^6 m^3$/h.



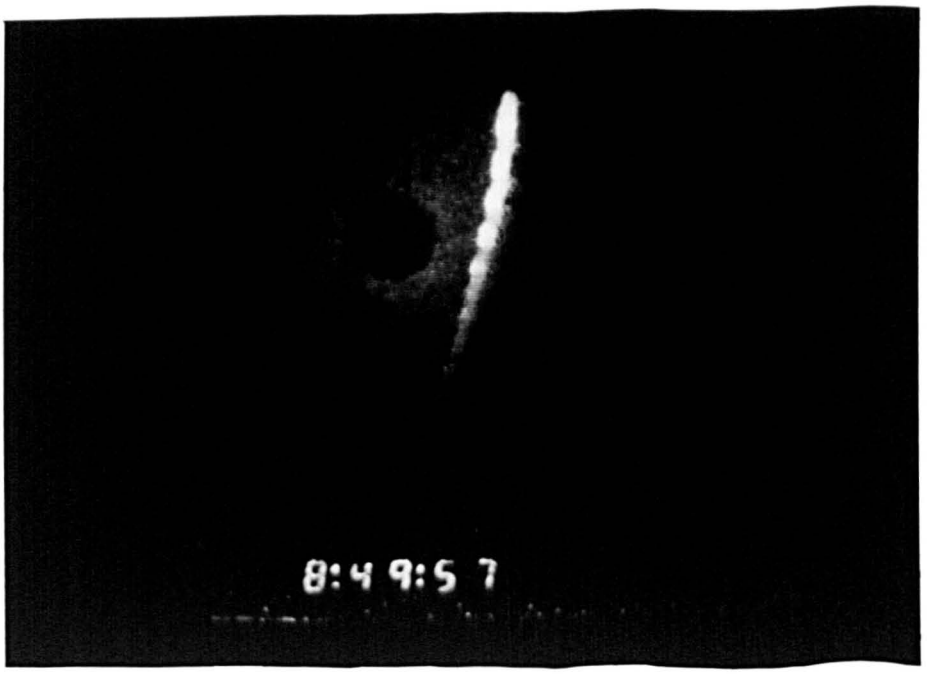
Narrow beam source, top view. Plate 1.



Light-pen system Plate 2.

Video recorder tracks of moth flight around 120K MV source, plan view (image intensified).

Plate 3



Video recorder tracks of moth flight around 120K MV source, plan view (image intensified).

Plate 4

Video recorder tracks of moth flight around 120K MV source, plan view (image intensified).

Plate 5